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Published in:
Geological Journal

DOI:
[10.1002/gj.3529](https://doi.org/10.1002/gj.3529)

Publication date:
2019

Citation for published version (APA):

Thomas, B. A., Appleton, P., Cleal, C. J., & Seyfullah, L. J. (2019). The distribution of plant fossils and their palaeoecology in Duckmantian (Bashkirian, Lower Pennsylvanian) strata at Brymbo, North Wales, UK. *Geological Journal*. <https://doi.org/10.1002/gj.3529>

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RESEARCH ARTICLE

The distribution of plant fossils and their palaeoecology in Duckmantian (Bashkirian, Lower Pennsylvanian) strata at Brymbo, North Wales, UK

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Handling Editor: I. Somerville

Plant fossils are recorded and described from Duckmantian clastic strata associated with coal seams in a small conserved area at Brymbo in the Wrexham (North Wales) coalfield. The exceptionally preserved flora consists of adpressions in mudstones, shales, and sandstones, more three-dimensionally preserved plant remains in ironstone nodules, and three-dimensionally preserved stems in their original positions of growth. The relationships of the plant fossils to the sediments are discussed and related to the varying conditions affecting the ecology of the area. Sometimes the influx of sediments was very rapid as can be seen by the numbers of erect and branching *Calamites*, arborescent lycophyte stems, and stigmarian bases preserved in sandstone in their original positions of growth.

KEYWORDS

Duckmantian, palaeoecology, plant fossils, sedimentology

1 | INTRODUCTION

During the Bashkirian and Moscovian times, extensive wetland forests grew on the Variscan foreland in tropical Euramerica. These were mostly dominated by arborescent lycophytes that produced large quantities of peat, which have since changed into thick coal deposits. Because of this change from vegetation to peat then coal, the assemblages of plants are often referred to as the coal forests. The fossil floras preserved in the coalfields of north-western Europe have been intensively studied for over two centuries, making them among the best known Palaeozoic floras in the world (e.g., see Cleal, 1997, 2005, 2007, 2018; Cleal, Opluštil, Thomas, & Tenchov, 2009; Cleal & Thomas, 1994, 1995; Josten, 1991; Laveine, 1986, for reviews).

However, the plant biodiversity of some of the coalfields is less well known. This paper summarizes the results of the analysis of a Duckmantian site at Brymbo in the Wrexham coalfield, in North Wales, where there are a variety of sedimentary rocks laid down between coal seams. The exceptionally well-preserved flora contains three-dimensionally preserved *Calamites* Brongniart, stigmarian bases, and lycophyte stems in their original positions of growth (Appleton, Malpas, Thomas, & Cleal, 2011; Thomas, 2014, 2016; Thomas & Seyfullah, 2015). In this paper, we document the remainder of the mainly allochthonous plant adpressions associated with these autochthonous stems.

2 | GEOLOGICAL SETTING

Brymbo is a village in the Denbighshire Coalfield in North Wales (UK) near the town of Wrexham (Figure 1) and lies in the western part of

This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

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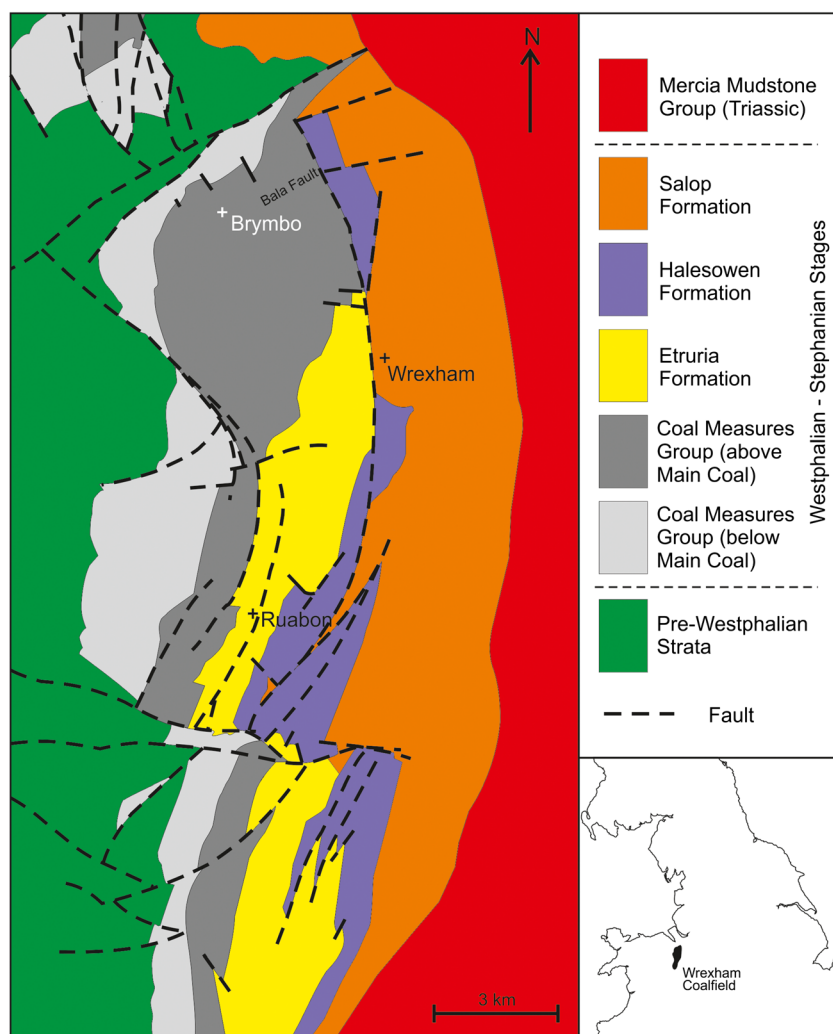


FIGURE 1 Geological map of the Denbigh Coalfield. Inset shows location of the coalfield in Britain. From Appleton et al. (2011) [Colour figure can be viewed at wileyonlinelibrary.com]

the Central Pennine Basin. The coalfield has a relatively condensed succession of Pennsylvanian (upper Carboniferous) strata overlying the Mississippian (lower Carboniferous) Clwyd Limestone Group and Silurian marine clastic sediments (Waters et al., 2011). The lower part of the Pennsylvanian succession (Figure 2) consists of grey coal-bearing beds of the Lower and Middle Pennines Coal Measures formations, deposited in a proximal, fluvio-lacustrine setting (Fielding, 1984a, 1984b, 1986). The area was part of the relatively stable, cratonic Pennine Basin where gentle down-warping provided accommodation space for sediment and coal accumulation, but there was little other tectonic disturbance (Cleal et al., 2009). The grey coal-bearing beds pass upwards into barren red-beds of the Etruria Formation (historically referred to here as the Ruabon Marl) that are probably Bolsovian in age and laid down at a time when lower water tables allowed some post-depositional secondary oxidation (Besly & Fielding, 1989; Besly & Turner, 1983).

Opencast mining at Brymbo worked coals of the Middle Pennines Coal Measures deposits (Duckmantian/"Westphalian B"/late Bashkirian in age). Although most of the opencast has been infilled with spoil from the adjacent steelworks, a small area of exposed Carboniferous rocks was conserved when an important assemblage of plant fossils was recognized. This exposure shows about 14 m of strata with two coal seams (the Crank Coal and the Two Yard Coal),

which for the purposes of this study have been divided into 13 beds (Figure 2). The start of the sequence is interpreted as deposits of a swamp floodplain covered with vegetation that was drowned by mud-laden floodwater. A fluvial delta then encroached across the lake permitting colonization by arborescent lycophytes and *Calamites*. Four or possibly five subsequent flooding events each resulted in the rapid deposition of several metres of sediment, which killed all the plants but also preserved some stems of lycophytes and *Calamites* in their original upright growth position (Appleton et al., 2011; Thomas, 2014).

The exposure was discovered prior to the original compilations of Geological Conservation Review (GCR) sites for Palaeozoic palaeobotany and Pennsylvanian (upper Carboniferous) stratigraphy (Cleal & Thomas, 1995, 1996). However, it has been subsequently added to the registered GCR sites and has been scheduled as a Site of Special Scientific Interest (SSSI).

3 | PLANT REMAINS AT BRYMBO

Representative specimens collected from Brymbo have been deposited in Amgueddfa Cymru—National Museum Wales, Cardiff (NMW), the distribution of plant fossils in the beds at Brymbo is summarized in

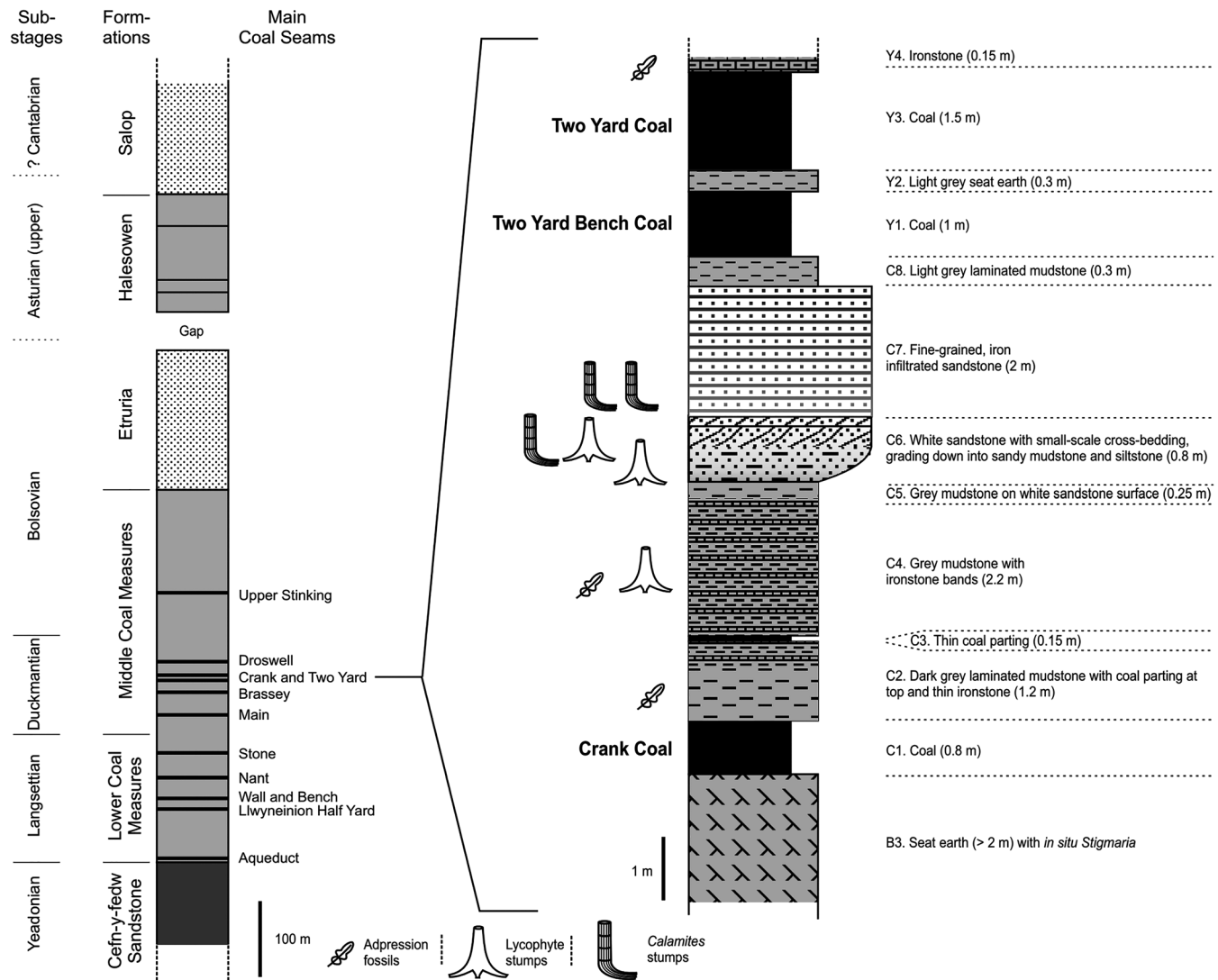


FIGURE 2 A generalized sequence through the Denbigh Coalfield succession showing the main coal seams, together with a detailed graphical log of the sequence exposed at Brymbo, and a guide to the beds referred to throughout the text. Langsett., Langsettian; Duckman., Duckmantian. Adapted from Appleton et al. (2011)

Table 1; further research is ongoing on many of these plants. A full inventory of the plant fossils is given in Data S1.

3.1 | The Brymbo *in situ* fossil trees

This site is perhaps best known for the *in situ* tree stumps found in beds C4, C6, and C7 (Figures 2 and 3). For further details of the calamite stems, see Thomas (2014), and of the lycophyte stems, see Thomas and Seyfullah (2015).

3.2 | Lycophyte stem and shoot fossils

3.2.1 | *Lepidodendron* Sternberg, 1820

Lepidodendron is one of several fossil genera of arborescent lycophyte stems characterized by persistent swollen leaf bases (leaf cushions) from which the more distal leaf laminae have usually been shed. The species

are distinguished on the overall shape of their cushions, which may be almost isodiametric to several times longer than broad, diamond-shaped leaf scars that may be isodiametric or broader than long, surface markings on the cushions, the position of the ligule pit aperture and the presence or absence of external parichnos. The lateral lines that usually run from the edge of the leaf scar to meet the cushion edge demarcate the upper and lower cushion surfaces (effectively the adaxial [upper] and abaxial [lower] surfaces of the leaf lamina). The two areas of cushion surface may be similar in appearance, or the upper surface may be finely striated. Cuticle studies can be a great help in species identification in showing epidermal cell size and shapes, stomatal sizes and distributions, and ligule pit cuticles (Thomas, 1966, 1970).

Lepidodendron aculeatum Sternberg, 1820

Only one specimen was found at Brymbo. It has large leaf cushions that are three to four times as long as broad, with curved upper and lower angles that join with the cushions above and below. Leaf scars

TABLE 1 Distribution of plant fossils within the Brymbo section

Species	B2	C2	C3	C4	C5	C6	C7	Y3	Y4
<i>Stigmaria ficoides</i>								9	
<i>Lepidodendron aculeatum</i>				1					
<i>Lepidodendron acutum</i>			3	8	1	3			
<i>Lepidodendron dichotomum</i>	1								
<i>Lepidodendron feistmantelii</i>				2					
<i>Lepidodendron lycopodioides</i>				1					
<i>Lepidodendron ophiurus</i>	2		1	23		11			
<i>Lepidodendron rimosum</i>								1	1
<i>Lepidophloios acerosus</i>				5		1			
<i>Lepidophloios laricinus</i>				1		3			
<i>Ulodendron majus</i>				1		4			
<i>Ulodendron landsburgii</i>				3					
<i>Omphalophloios feistmantelii</i>	15		1	1	1	2			
<i>Flemingites</i> sp.	1			16	2	8			
<i>Lepidostrobohyllum</i> sp.				8					2
<i>Lepidostrobohyllum hastatum</i>				1		1			
<i>Lepidostrobohyllum lanceolatum</i>				2					
<i>Calamites suckowii</i>				2		7			
<i>Calamites cistii</i>				9		6			
<i>Annularia galioides</i>						2			
<i>Annularia radiata</i>				5					
<i>Annularia fertilis</i>				2					
<i>Annularia</i> sp.				3					
<i>Asterophyllites charaeformis</i>				2					
<i>Asterophyllites equisetiformis</i>				4					
<i>Palaeostachya ettingshausenii</i>				2					
<i>Calamostachys</i> sp.						1			
<i>Sphenophyllum majus</i>				7		2			
<i>Sphenophyllostachys</i> sp.				1					
<i>Zeilleria fosteri</i>				28					
<i>Karinopteris jacquotii</i>				31		5			1
<i>Alethopteris urophylla</i>									4
<i>Neuropteris semireticulata</i>		1		5		1			1
<i>Paripteris pseudogigantea</i>		1		1					6
<i>Aulacotheca elongata</i>									2
<i>Trigonocarpus</i>									3
<i>Cordaitea</i> sp.		1		2		1			1
<i>Pinnularia</i> sp.				3					1

Note. Beds as designated in Figure 2.

are a little above the middle of the cushions and are about as long as broad with three foliar scars. Ligule pit apertures are immediately above the leaf scars, and there are two external parichnos below the scars. Central keels are above and below the leaf scar, with the upper

keel interrupted by a notch and the lower keel dissected by distinct grooves. Lateral lines curve from the edges of the leaf scar to meet the cushion edges about one-third of the distance up the leaf cushion. The leaf cushions on some specimens are separated by narrow strips crossed with ridges and grooves shown to represent secondary expansion of the epidermal and subepidermal cells (Thomas, 1970). This species is very common throughout the Pennsylvanian and has been recorded from all the major Euramerican coalfields, from the Chokierian (upper Namurian) to the Asturian substages (Álvarez-Vásquez & Wagner, 2014; Crookall, 1964; Thomas, 2007; Thomas & Tenchov, 2004; Figure 4).

***Lepidodendron acutum* (Presl in Sternberg) Kidston, 1911 (=Bergeria acuta Presl in Sternberg, 1838)**

These are leafy stems with elongated leaf cushions that have acute upper angles, blunt pointed bases, and gently rounded sides (Figure 5a–d). The leaf laminae depart at less than 45° to the stem axis, are broader than 3 mm at the base, and are S-shaped. Sometimes the leaf laminae have been pulled off during the splitting of the rock leaving only a curved line visible near the apices. These are not true leaf scars but can be referred to as pseudoscars. This species has been recorded from all the major Euramerican coalfields and from the Langsettian to the Asturian (Crookall, 1964; Thomas, 2007; Thomas & Tenchov, 2004).

Álvarez-Vásquez and Wagner (2014) and Álvarez-Vásquez, Bek, Knight, and Wagner (2018) transferred all leafy stems of arborescent lycophytes to the genus *Bergeria* Presl in Sternberg, 1838, defining it as “lycopsid stems covered with spirally arranged, rhomboidal leaf cushions, longer than broad, contiguous or separated by narrow grooves, and without a differentiated leaf scar. Leaves linear-lanceolate, entire, single-veined.” They argued that commonly encountered species such as *L. acutum* Presl in Sternberg, 1838 *Lepidodendron ophiurus* Brongniart, 1822), *Lepidodendron lycopodioides* Sternberg, 1821, and even *Ulodendron* Lindley and Hutton, 1831, should be transferred to *Bergeria*. However, interpreted in this way, all leafy lycophyte shoots with attached cones would also be included in *Bergeria* which to us does not seem logical. Álvarez-Vásquez and Wagner (2014) added the comment that “the shape and size of the leaf scar to be due to the position of the leaf with regard to the leaf cushion and to the kind of leaf base, which may be either narrow or more laterally extensive.” We believe that the line near the top of the leaf cushion would be better described as a “false leaf scar” as done by Chaloner (1986a, 1986b, 1967, p. 533) because many leafy stems lose their laminae when the rock is split. It is most likely that all parts of arborescent lycophytes were originally leafy and only when the taller, maturing plants started to branch that their lower parts would have been shaded, with a subsequent reduced ability to photosynthesize, prompting the loss of leaf laminae (Thomas & Cleal, 2017).

***Lepidodendron dichotomum* Sternberg, 1820**

Just a single specimen of this species was found at Brymbo (Figure 6). It has leaf cushions that are roughly diamond-shaped and approximately as broad as long, with their leaf scars broader than long, and about one-third of the distance down the leaf cushion. There are three



FIGURE 3 Field photographs of *Stigmara* in situ at Brymbo; both photos by B. A. Thomas circa 2010. (a) Exposure face with a stem cast with stigmarian base (left) and the mould of another (right), both rooted in the same level. (b) *Stigmara* and trunk in situ. Yellow measure 1 m long [Colour figure can be viewed at wileyonlinelibrary.com]

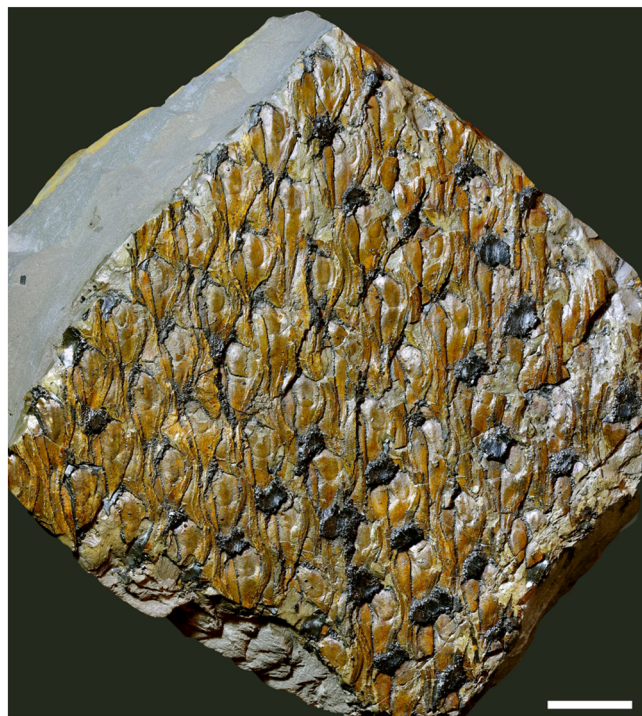


FIGURE 4 *Lepidodendron aculeatum* Sternberg, 2013.43G.88, bed C4. Scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

foliar prints, and the ligule pit aperture is adjacent to the upper angle of the leaf scar. Keels are present above and below the leaf scars and lateral lines curve downwards from the lateral angles of the leaf scar to the edges of the cushion. The leaf cushion is finely striated above the leaf scars and smooth below. Intrafoliar parichnos are present below the leaf scars, although they are sometimes rather indistinct. This species has been previously recorded from the Langsettian of the Yorkshire Coalfield (Thomas, 1970), the Asturian of the Pennines, South Wales,

and the Radstock coal fields in the United Kingdom, Bohemia (Czech Republic), Zwickau (Germany), and Dobrudzha (Bulgaria) (Thomas, 1970; Thomas in Cleal et al., 2009).

Lepidodendron feistmantelii Zalessky, 1904

Leaf cushions are rhomboidal, longer than broad, and not continuous with cushions above and below. The leaf scars are in the centre of the cushions and raised above the cushion surface. Impressions as found at Brymbo show no leaf scars as they are below the surface of the sediment (Figure 7a–c; compare with Thomas, 1970, text figure 6). Cushions have prominent keels above and below the leaf scars and equally prominent lateral lines running straight to the angles of the leaf cushions. This species has been previously recorded from the Langsettian and Bolsavian of the Yorkshire Coalfield (Thomas, 1970), the Asturian of the Pennines Coalfield (Thomas in Cleal et al., 2009), Canada (Bell, 1944), and France (Bureau, 1914).

Lepidodendron lycopodioides Sternberg, 1823

Specimens referable to this species are leafy stems with no obvious leaf cushions. The leaf laminae depart at less than 45° to the stem axis and curved upwards. It is the shape of the leaves that distinguish this species from *L. acutum* described above, and the angle of departure distinguishes it from *Lepidodendron ophiurus* Brongniart below. This species is common and found at many horizons throughout most coalfields. However, they almost certainly represent leafy shoots from more than one biological species so attempting to record its distribution would be rather meaningless. Future research on such leafy shoots involving epidermal details may distinguish meaningful species that could be useful stratigraphic markers (Figure 8).

Lepidodendron ophiurus Brongniart, 1822

These are leafy shoots with small longitudinally elongated, rhomboidal to fusiform leaf cushions from which the leaves depart at right

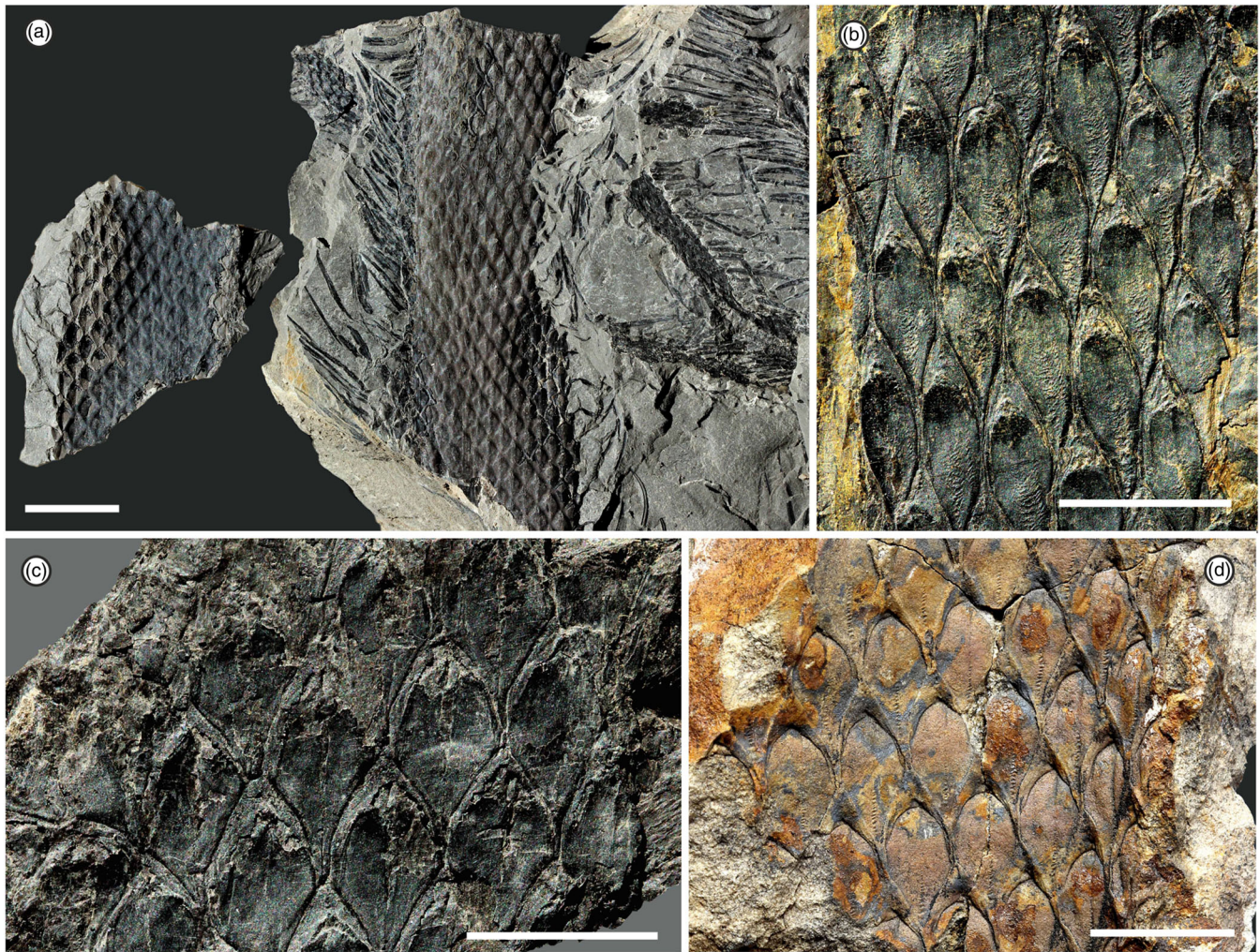


FIGURE 5 *Lepidodendron acutum* (Presl) Kidston, stems. (a) 2013.43G.143.1-2, bed C4, scale bar = 20 mm. (b) 2013.43G.130, bed C3, scale bar = 10 mm. (c) 2013.43G.133, bed C3, scale bar = 10 mm. (d) 2013.43G.131, bed C6, scale bar = 5 mm [Colour figure can be viewed at wileyonlinelibrary.com]

angles from about a third of the way down before turning upwards through almost a right angle (Figure 9a–e; Thomas & Seyfullah, 2015). Branching was shown by several shoots, such as Figure 9a, which show a main axis dichotomizing but with a leafy side branch departing at a right angle (presumably a pseudodichotomy) that itself dichotomizes. Other specimens show simple dichotomies ranging between 20° and 50° (e.g., Figure 9b,c). Leaf cushion surfaces are smooth, although a few faint cross striations may sometimes be visible across the lower half. The leaf laminae are linear, single veined, and gradually taper to a point. The laminae are usually missing on the near surfaces of the stems, having been removed as the shale was split. False “leaf scars” are then left on the leaf cushions (rather than true leaf scars formed by leaf abscission). Lateral lines depart from the edges of these pseudoscars and extend to edges at the middle of the cushions. One specimen (Figure 16b) shows a shoot with a cone attached.

This is one of the more common lycophyte shoots at Brymbo that have been found in many beds in the sequence. It has also been

previously recorded from Duckmantian strata of Yorkshire, Bolsovian strata of Lanarkshire (Thomas & Seyfullah, 2015), and Asturian strata of southern Britain, the Pennines, Bohemia (Czech Republic), and Dobrudzha (Bulgaria) (Thomas in Cleal et al., 2009).

***Lepidodendron rimosum* Sternberg, 1820**

Leaf cushions are elongated, straight, and more or less symmetrical and separated by areas of inter-cushion areas. Leaf scars are in the upper half of the cushions. The Brymbo specimens appear decorticated and their assignment to this species relies on the size, shape, and positioning of the subepidermal remains of the leaf cushions. Crookall (1964) described this species as being most common in the Langsettian and fairly frequent in the Duckmantian and very rare in the Bolsovian and Asturian in the British Coalfields. The holotype is from the Bolsovian of the Radnice Member, Kladno Formation, Bohemia. It is also known from the Asturian of the Appalachians (USA), Sydney (Canada), Southern Britain, and Donetz (Ukraine) coalfields (Thomas, 2007; Figure 10).



FIGURE 6 *Lepidodendron dichotomum* Sternberg bark fragment, 2013.43G.124, bed B2, scale bar = 5 mm [Colour figure can be viewed at wileyonlinelibrary.com]



FIGURE 8 *Lepidodendron lycopodioides* Sternberg, leafy shoots, 2013.43G.108, bed C4, scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

3.2.2 | *Lepidophloios* Sternberg, 1825

Confusion has existed between the separation of *Lepidophloios* and *Lepidodendron*, and opinions have varied about the generic determination of some specimens especially when specimens are mistakenly illustrated in an inverted position. However, *Lepidophloios* clearly differs from *Lepidodendron* by having its leaf cushions characteristically bulging outwards and deflected downwards so that the leaf scars are

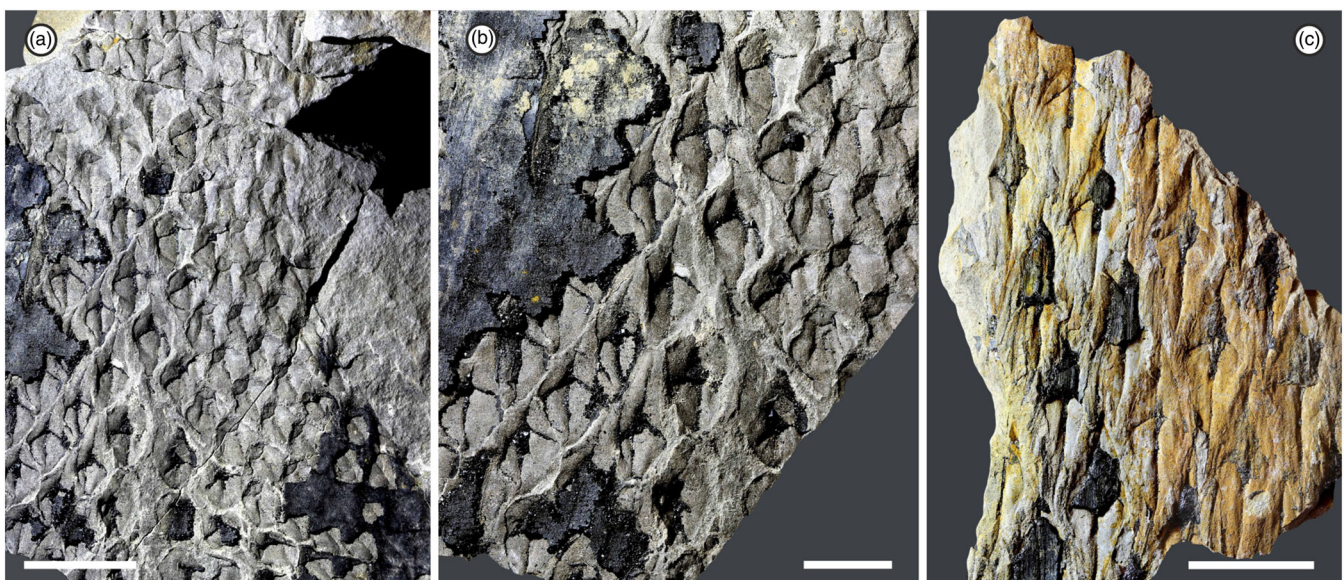


FIGURE 7 *Lepidodendron feistmantelii* Zalesky, bark fragments. (a–b) 2013.43G.89, bed C4; (a) scale bar = 20 mm; (b) scale bar = 10 mm. (c) 2013.43G.145, bed C4, scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

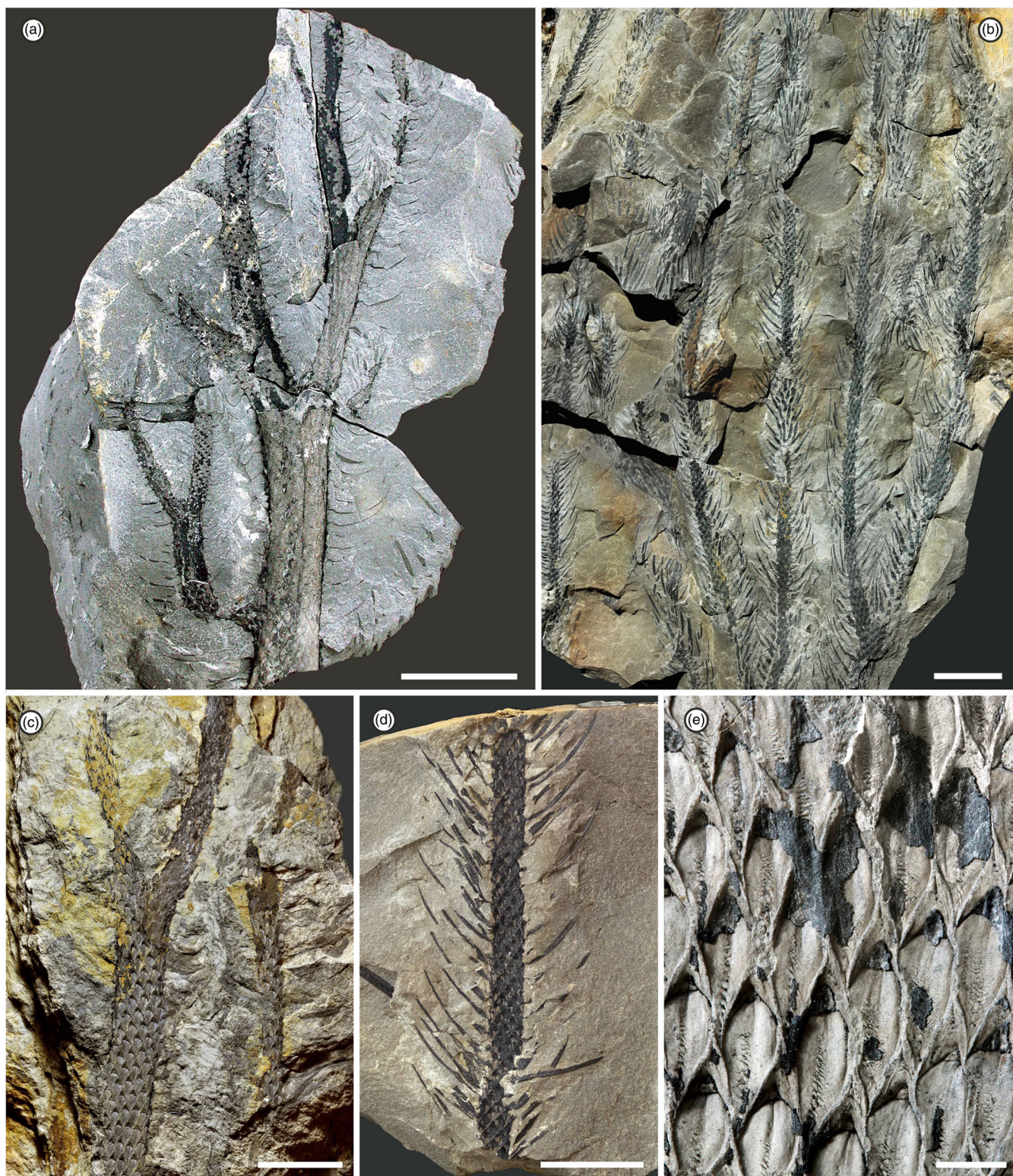


FIGURE 9 *Lepidodendron ophiurus* Brongniart, various fragments of the plant from Brymbo, all from bed C4. (a–c) Dichotomizing shoot; (a) 2013.43G.68A, scale bar = 50 mm; (b) 2013.43G.147, scale bar = 25 mm; (c) 2013.43G.76, scale bar = 20 mm. (d) Leafy shoot, 2013.43G.70A, scale bar = 20 mm. (e) Bark impression, 2013.43G.72.1, bed C4, scale bar = 5 mm [Colour figure can be viewed at wileyonlinelibrary.com]



FIGURE 10 *Lepidodendron rimosum* Sternberg, bark impression, 2013.43G.246, bed Y3, scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

at the lowest concealing the lower surface of the cushion. The bulging and downward deflection of the leaf cushions is an expression of their subsequent growth (Thomas, 1977).

***Lepidophloios acerosus* (Lindley & Hutton) Kidston, 1890 (= *Lepidodendron acerosum* Lindley & Hutton, 1831)**

This species has leaf cushions that are characteristically elongated and bulging downwards (Figure 11a–c). The leaf scars at the lower points of the cushions are broader than long and have three foliar prints. The ligule pit apertures occur just above the leaf scars. Distinct central keels are usually visible on the leaf cushions although in some specimens they are only slightly raised. The species has been previously recorded from the Langsettian of Yorkshire, Lancashire, and Lanarkshire, the Duckmantian of Yorkshire, South Wales, and Lancashire, the Bolsovian of Kent (Thomas, 1977), and the Asturian of the Pennines, Southern Britain, Bohemia (Czech Republic), and Dobrudzha (Bulgaria) (Thomas in Cleal et al., 2009).

***Lepidophloios laricinus* (Sternberg) Sternberg, 1825 (= *Lepidodendron laricinum* Sternberg, 1820)**

Leaf cushions of specimens referred to this species have broad, downward bulging and overlapping leaf cushions. The visible portions of the leaf cushions are normally much broader than long although very occasionally they are nearly equal. The leaf scars, situated at the lower angle of the cushions, are broader than long and possess three foliar prints. Indistinct ligule pit apertures are a short distance above the leaf scars. The cushions occasionally bulge in the median line giving the appearance of a very indistinct keel. Figure 12a shows an unusual specimen with several lateral branches, some only represented by rounded scars indicating their departures at approximately right angles to the fracture plane.

The species has been previously recorded from the Langsettian of Yorkshire, Lancashire, and Lanarkshire, the Duckmantian of Yorkshire, South Wales, and Lancashire, the Bolsovian of Kent (Thomas, 1977), the Asturian of the Pennines, Southern Britain, Bohemia (Czech Republic), and Dobrudzha (Bulgaria; Thomas in Cleal et al., 2009; Figure 12a–c).

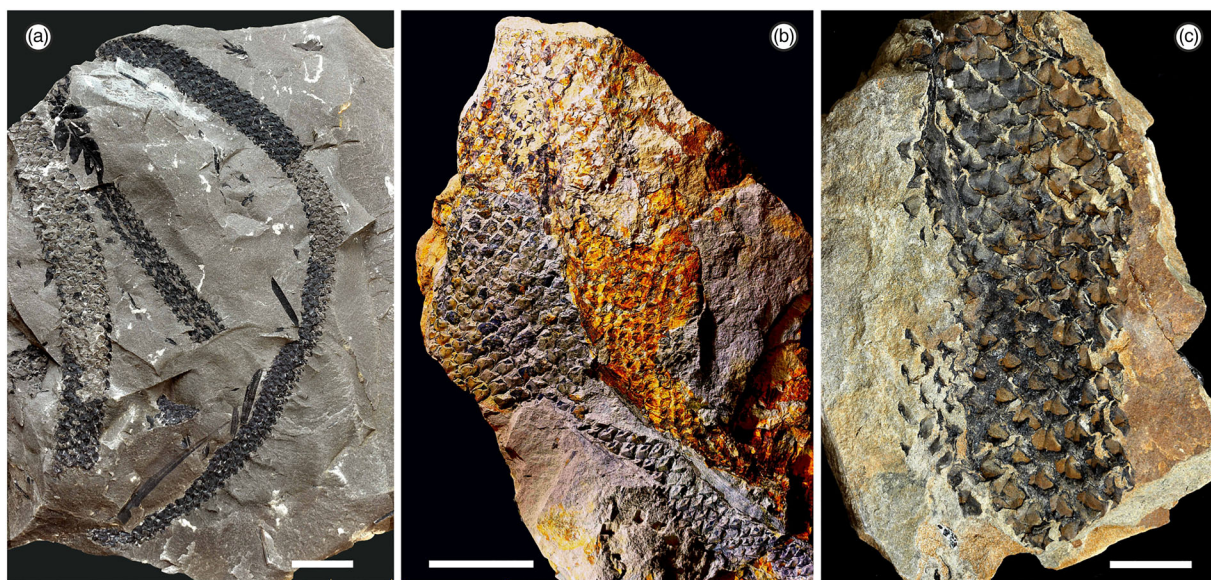


FIGURE 11 *Lepidophloios acerosus* Lindley & Hutton. (a) Leafy shoots, 2013.43G.136, bed C4, scale bar = 20 mm. (b,c) Bark fragments; (b) 2013.43G.97, bed C6, scale bar = 50 mm; (c) 2013.43G.96, bed C6, scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

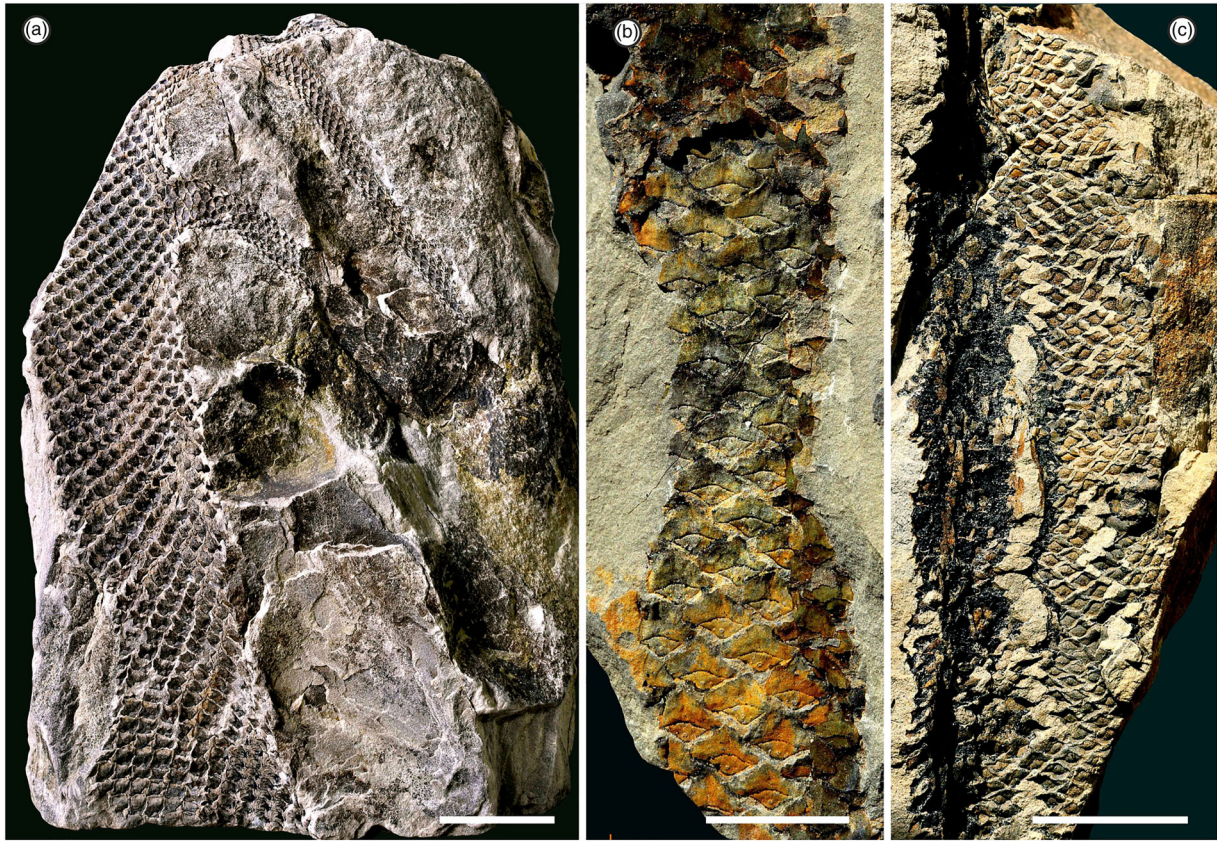


FIGURE 12 *Lepidophloios laricinus* Sternberg, branches and bark fragments. (a) Shoot with two pendulous branches, 2013.43G.269, bed unknown, scale bar = 50 mm. (b–d) Bark; (b) 2013.43G.146, bed C6, scale bar = 10 mm; (c) 2013.43G.98, bed C4, scale bar = 5 mm; (d) 2013.43G.138, bed C6, scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

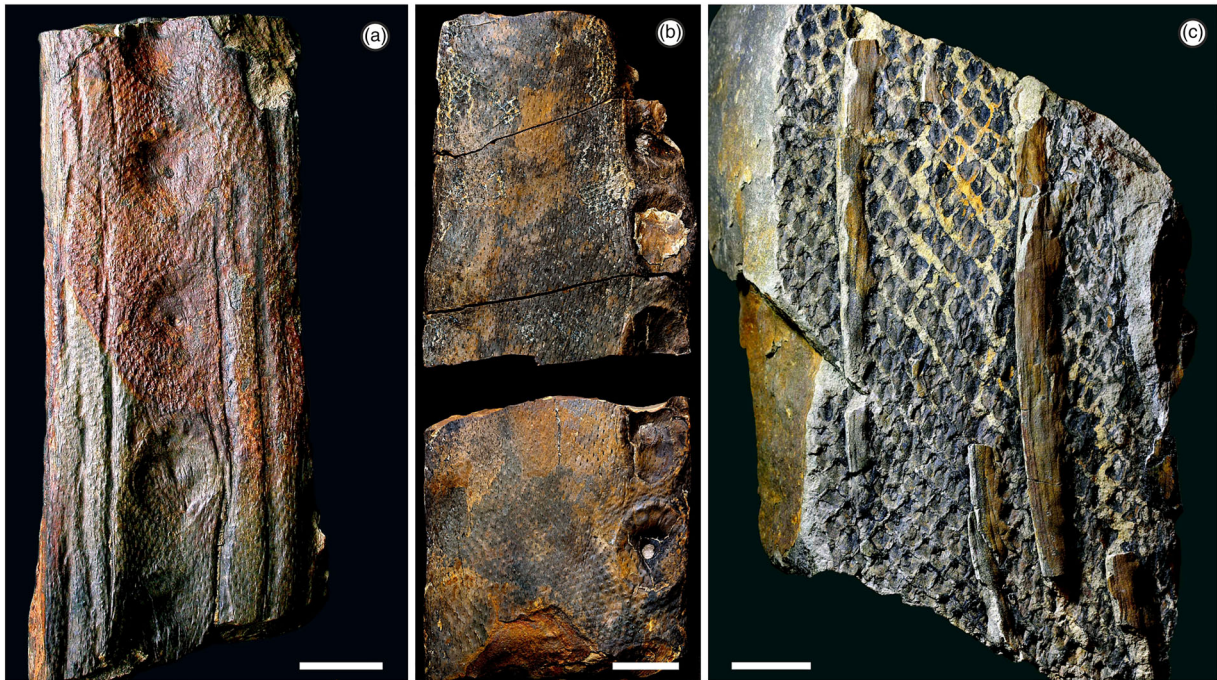


FIGURE 13 *Ulodendron* Lindley & Hutton. (a,b) *Ulodendron majus* Lindley & Hutton; (a) 2013.43G.281, bed C6, scale bar = 50 mm; (b) 2013.43G.101, bed C4, scale bar = 20 mm. (c) *Ulodendron landsburgii* (Kidston) Thomas, 2013.43G.278.1–2, bed C6, scale bar = 40 mm [Colour figure can be viewed at wileyonlinelibrary.com]

3.2.3 | *Ulodendron* Lindley & Hutton, 1831

Ulodendron is characterized by its retention of narrow short laminae on rhomboidal leaf cushions. The better preserved specimens show ligule pits positioned in the upper angles of their leaf cushions as short narrow ridges running down from the upper angles of the cushions. Maceration clearly reveals the ligule pits (Thomas,

1967). There are two recognizable species of *Ulodendron* found at Brymbo. There are also large stems with indistinct, diamond-shaped leaf base outlines suggesting they are most likely to belong to *Ulodendron*.

As stated above, we do not accept the view of Álvarez-Vásquez and Wagner (2014) that all leafy shoots should be included in the genus *Bergeria*, preferring to continue using the genus *Ulodendron*.

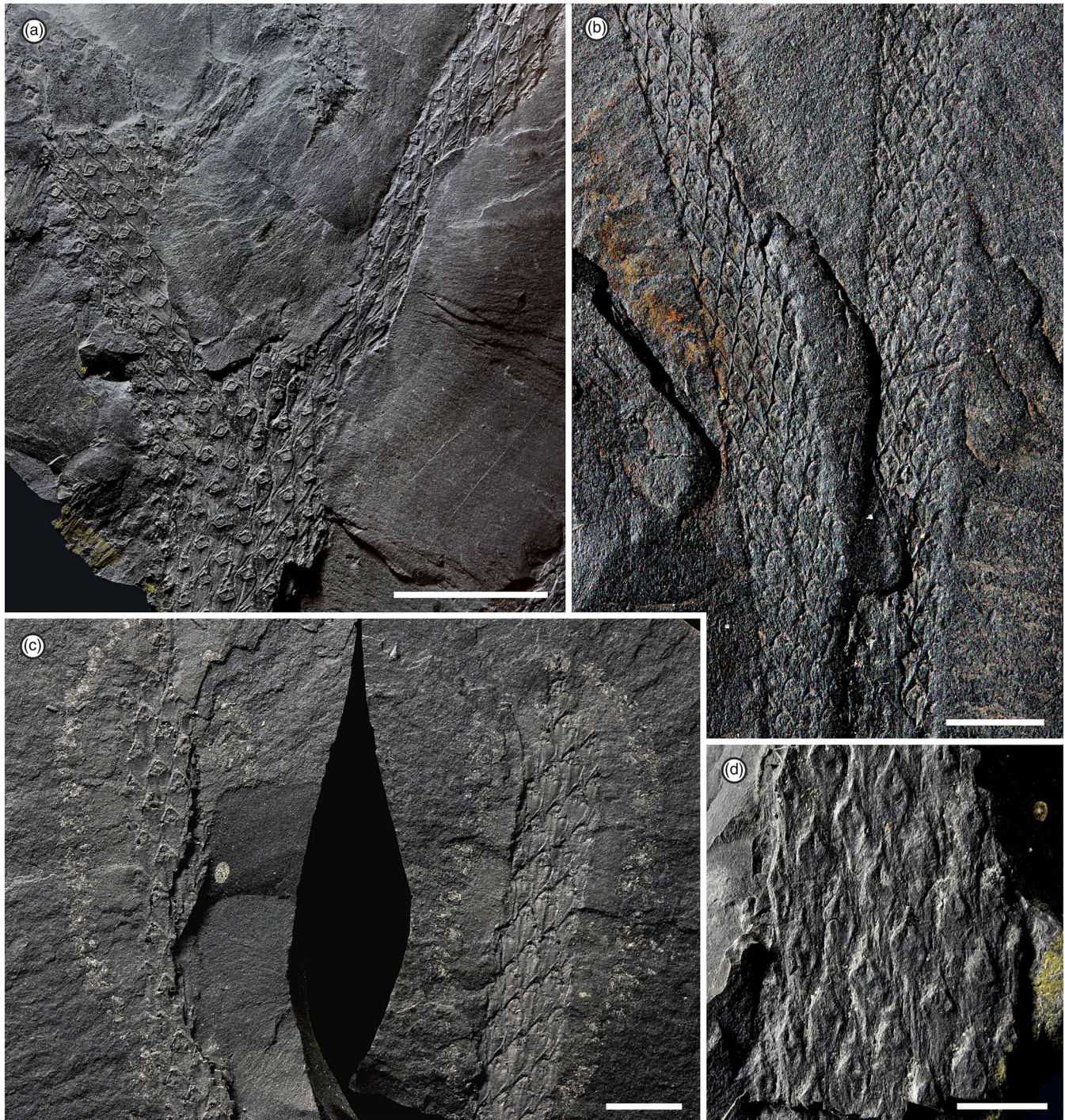


FIGURE 14 *Omphalophloios feistmantelii* (O. Feistmantel) Bek et al., shoots, scale bars = 5 mm except (a). (a) 2013.43G.164, bed B2, scale bar = 20 mm; (b) 2013.43G.165, bed B2; (c) 2013.43G.168, bed B2; (d) 2013.43G.167, bed B2 [Colour figure can be viewed at wileyonlinelibrary.com]

Ulodendron majus Lindley & Hutton, 1831

The leaf cushions are rhomboidal, slightly broader than long, and separated by narrow grooves (Figure 13a,b). The species has been previously recorded from an unknown horizon in Kilmarnock, Ayrshire, Scotland; and the Asturian of South Wales; the Sydney Coalfield, Nova Scotia, Canada; and the Donetz, Ukraine (Thomas, 1967).

Ulodendron landsburgii (Kidston) Thomas, 1968 (= *Lepidodendron landsburgii* Kidston, 1893)

The leaf cushions are rhomboidal, about twice as long as broad, separated by narrow grooves and areas of flat stem above each leaf cushion. All the specimens of this species show the characteristic elongated shape of the leaf bases. The figured specimen (Figure 13c) shows longitudinal infilling by sediment indicating signs of secondary growth with subsequent splitting of the outer tissues. This species has previously only been recorded from the lower Westphalian of the central coalfields of Scotland (Thomas, 1968).

3.2.4 | *Omphalophloios* D. White, 1898

Omphalophloios is a genus of Pennsylvanian subarborescent lycopsid stems that dichotomizes several times. The basal part of the stems are vegetative bearing rhomboidal leaf cushions with rounded-shaped leaf scars, although the larger parts of the stems are fertile bearing oval sporangia in the axils of long grass-like laminae. The fertile zone matured from bottom to top shedding the laminae and then the ripened sporangia, leaving only pedicels on the naked axis. In situ megaspores can be assigned to the genus *Zonalesporites* (Ibrahim) Oshurkova and microspores to the genera *Cristatisporites* (Potonié & Kremp) Butterworth et al. and *Densosporites* (Berry) Butterworth et al. Bek, Opluštil, Drabková, and Pšenička (2015) interpreted *Omphalophloios feistmantelii* as a plant having an

opportunistic life strategy which enabled it to rapidly colonize habitats, particularly where there was limited competition, preferring peat and mixed peat-clastic swamps.

Omphalophloios feistmantelii (O. Feistmantel) Bek et al., 2015 (= *Sigillariaestrobis feistmantelii* O. Feistmantel, 1875)

The leaf cushions on the Brymbo specimens are symmetrical to slightly asymmetrical with neither a central keel nor parichnos markings. The leaf scars are more or less in the middle, or slightly above the middle, of the leaf cushions and are roughly subtriangular in shape with a single vascular scar Figures 14a–d. There are four specimens showing fertile zones with sporangia attached to the shoot (three figured, Figures 15a–c).

The species has previously been recorded from the Bolsovian of several localities in the Late Palaeozoic basins of central and western Bohemia. Most of the specimens there are preserved in volcanoclastic rocks of the Velká opuka Tonstein and the Z-tuff bed, with a very few specimens preserved in mudstone (Bek et al., 2015).

3.3 | Isolated lycophyte leaves

3.3.1 | *Cyperites* Lindley & Hutton, 1832

These are very long, slender grass-like sterile leaves with a very few longitudinal ridges and furrows, pointed at the apex and enlarged at the base, that probably belong to *Sigillaria*. There are two species of leaves that are most commonly described in the literature that are separated on their different margins: commoner *C. bicarinatus* Lindley & Hutton, 1831 with entire margins and the much rarer *C. ciliatus* Crookall, 1966 with ciliated margins. The Brymbo specimens all correspond to the former (Figure 16a). The species is common and occurs throughout the Westphalian Stage (Langsettian–Asturian).

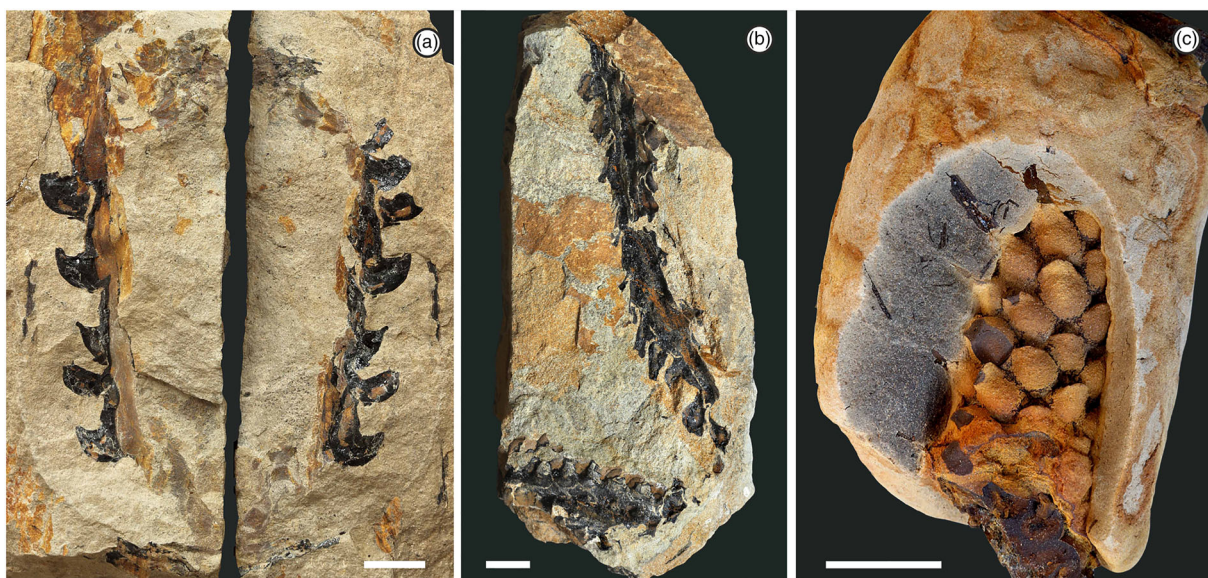


FIGURE 15 *Omphalophloios feistmantelii* (O. Feistmantel) Bek et al., fertile zones, all scale bars = 10 mm. (a) 2013.43G.162, bed C6; (b) 2013.43G.163, bed C6; (c) 2013.43G.265, bed C4 [Colour figure can be viewed at wileyonlinelibrary.com]

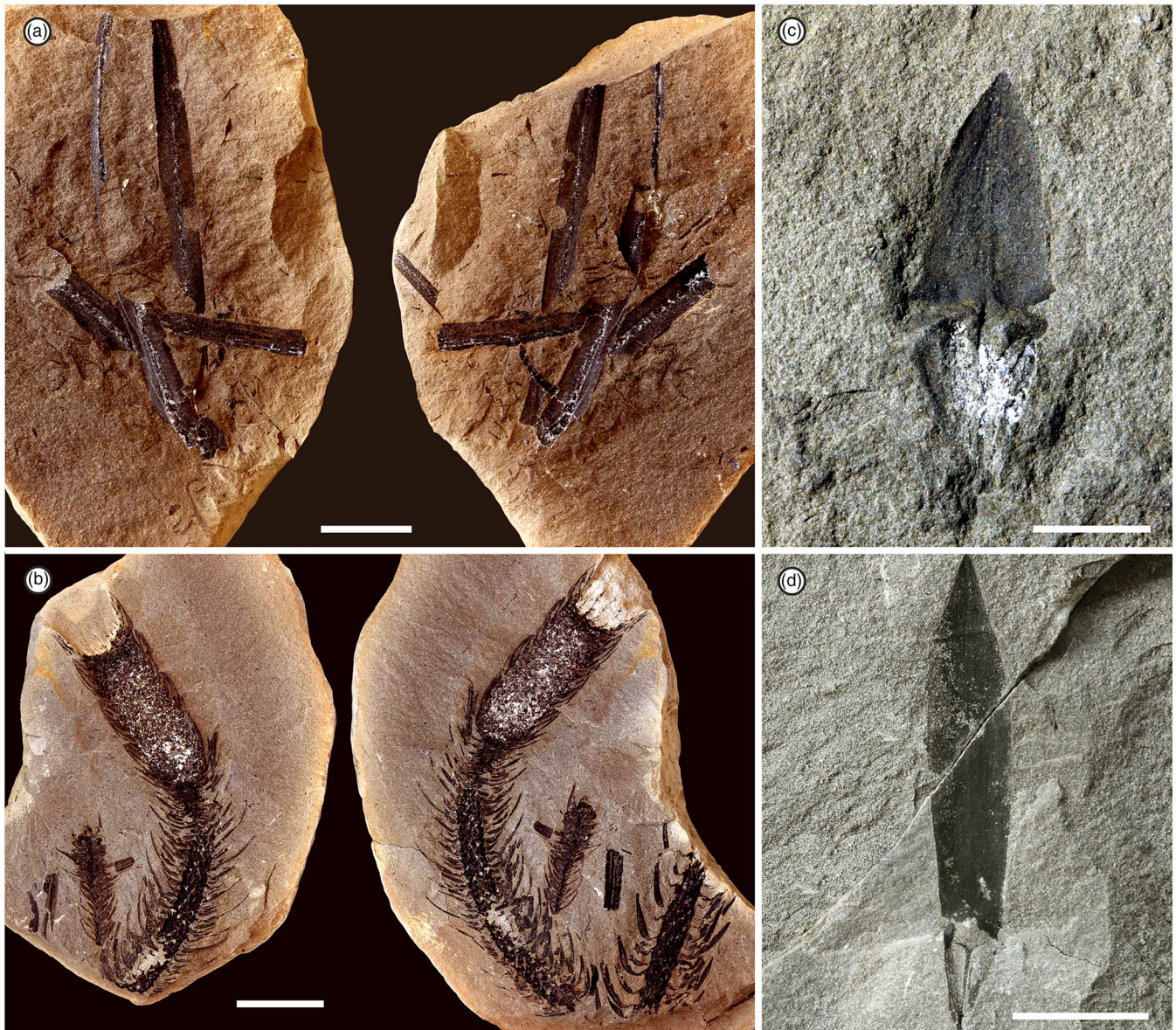


FIGURE 16 Lycopphyte fragments, all from bed C4. (a) *Cyperites* Lindley and Hutton, 2013.43G.282, scale bar = 10 mm. (b) Lycopphyte cone attached to *Lepidodendron ophiurus* Brongniart, leafy shoot, 2013.43G.120, scale bar = 20 mm. (c) *Lepidostrobophyllum hastatum* (Lesquereux) Chaloner, 2013.43G.261, scale bar = 5 mm. (d) *Lepidostrobophyllum lanceolatum* (Lindley and Hutton) Bell, 2013.43G.264, scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Lycopphyte fructifications

A number of lycopphyte fructifications were found at Brymbo with some attached to recognizable leafy shoots (e.g., Figure 16b). These are the subject of ongoing taxonomic research that will probably enable them to be referred to species of both *Lepidostrobus* and *Flemingites*.

3.4.1 | *Lepidostrobophyllum* (Hirmer) Allen, 1961

These are isolated sporophylls from lycopphyte cones, consisting of a basal (proximal) pedicel and an apical (distal) leaf-like lamina. Some possess pedicels with one large sporangium attached to their upper surfaces and remnants of the cone axis may be seen attached to their proximal ends. Others are only fragments of laminae. Thomas (1981) suggested that

the adaptation and specialization of the simpler units found in the free-sporing heterosporous cones enabled the plants to compete more successfully in establishing plant communities. The wing-like sporophyll lamina is thought to have been an adaptation for wind dispersal, a view supported by Habgood, Hemsley, and Thomas (1998).

Features used to distinguish species of *Lepidostrobophyllum* are the overall shape and size of the lamina and the shape of its apex, the shape of the pedicel, and the sporangium on its upper surface.

Lepidostrobophyllum hastatum (Lesquereux) Chaloner, 1967 (= *Lepidophyllum hastatum* Lesquereux, 1858)

These are more or less triangular-shaped sporophylls with incurved sides that have an out-turned lobe on either side of the lamina base (Figure 16c). *Lepidostrobophyllum alatum* Boulter is a



FIGURE 17 *Calamites* stems and pith casts. (a–c) *Calamites cystii* Brongniart; (a) 2013.43G.13, bed C4, scale bar = 20 mm; (b) 2013.43G.17, bed C4, scale bar = 20 mm; (c) 2013.43G.7 and 2013.43G.9, bed C6, scale bar = 20 mm. (d–f) *Calamites suckowii* Brongniart; (d) stem cast in sandstone photographed in the field, specimen not collected, bed C6, scale bar = 40 mm; (e) Cast and mould of a stem showing these different preservational types, 2013.43G.1, bed C4, scale bar = 20 mm; (f) branch cast in sandstone, 2013.43G.24, bed C6, scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

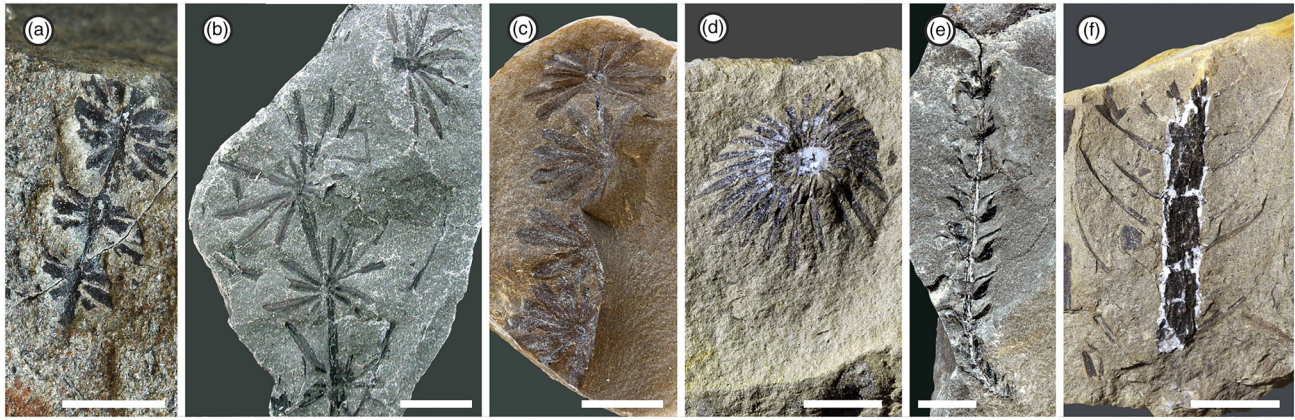


FIGURE 18 Leaves of calamites. (a) *Annularia galioides* (Lindley and Hutton) 2013.43G.32, bed C6, scale bar = 3 mm. (b) *Annularia radiata* (Brongniart) Sternberg 2013.43G.30, bed C4, scale bar = 10 mm. (c) *Annularia fertilis* Sternberg, 2013.43G.37, bed C4, scale bar = 5 mm. (d) *Annularia* sp., 2013.43G.29, bed C4, scale bar = 10 mm. (e) *Asterophyllites charaeformis* (Sternberg) Göppert, 2013.43G.33, bed C4, scale bar = 5 mm. (f) *Asterophyllites equisetiformis* Geinitz, 2013.43G.241, bed C4, scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

very similar species but with longer sporophylls and smaller wedge-shaped apical sporophylls.

This species is rare in Britain, and previously known from the Asturian of the Bristol and South Wales coalfields, and the Bolsovian of Kent (Crookall, 1966). Thomas (2007) has recorded the species from the Asturian of the Appalachians, Illinois, and Iberia.

***Lepidostrobophyllum lanceolatum* (Lindley & Hutton) Bell, 1938 (= *Lepidophyllum lanceolatum* Lindley & Hutton, 1831)**

These lanceolate sporophylls with an acute apex are much larger than *L. hastatum* (Figure 16d). This is a common species in the Pennsylvanian of Britain (Crookall, 1966). Thomas (2007) has recorded it from most Asturian coalfields, from the Appalachians (USA) to Dobrudzha (Bulgaria).

3.5 | Sphenophyte stems and leaves

3.5.1 | *Calamites* stems

The identification of *Calamites* at species level is based upon a number of internodal and nodal characters, including the number and distribution of branches. Arber (1918) took the view that the taxonomy of *Calamites* pith casts is often guesswork and that in many cases, it is impossible. Nevertheless, the tapering branches at Brymbo (in beds C4 and C6) are virtually identical to the figure of the type specimen of *Calamites suckowii* Brongniart (Figure 17a–f).

Compressions of branching *Calamites* found in the shales above the sandstone are probably the more apical parts of the stems preserved as pith casts; these are better included in the species *Calamites cistii* Brongniart. Other *Calamites* stems recovered from ironstone (siderite) nodules at Brymbo have leaves attached to the nodes showing them to represent the outer surface of a stem (Thomas, 2014, figure 13; here Figure 17e).

3.5.2 | Calamite foliage

Calamite leaves are elongate, linear, or lanceolate with a single vein and arranged in whorls around the stems. *Annularia* has linear-lanceolate or spatulate leaves that are broadest in the middle or upper half. *Asterophyllites* has more linear leaves that are either parallel sided or broadest in the proximal one-third.

***Annularia galioides* (Lindley and Hutton) Kidston, 1891 (= *Asterophyllites galioides* Lindley & Hutton, 1832)**

There are two specimens showing planar whorls of small, spatulate leaves typical of *A. galioides*. Crookall (1969) records it from the Duckmantian of many of the British coalfields, the Bolsovian of Cumberland and South Ayrshire and the Asturian of North Staffordshire (Figure 18a).

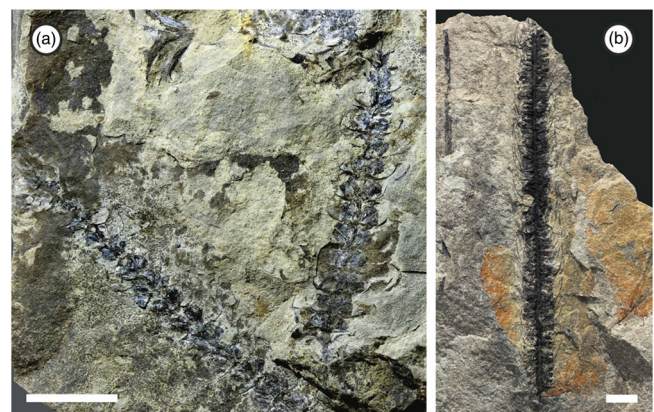


FIGURE 19 Calamite cones. (a) *Palaeostachya ettingshausenii* Kidston, 2013.43G.245, bed C4, scale bar = 10 mm. (b) *Calamostachys* sp., 2013.43G.251, bed C6, scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

***Annularia radiata* (Brongniart) Sternberg, 1825 (= *Asterophyllites radiata* Brongniart, 1822)**

This species has large, linear leaves that are broadest in the middle and have acuminate apices (Figure 18b). Crookall (1969) recorded it from the Langsettian to the Bolsovia of the British coalfields.

***Annularia fertilis* Sternberg, 1825**

This species has not previously been reported from the United Kingdom (Figure 18c). It bears some similarity to *Annularia sphenophylloides* (Zenker) Gutbier in having swollen leaves with a mucronate tip. However, *A. fertilis* has more lanceolate, rather than spatulate leaves. Moreover, *A. sphenophylloides* also tends to occur in rather younger floras, typically not occurring below the middle Bolsovia Substage (e.g., as in South Wales, Cleal, 2007).

***Annularia* sp.**

A number of specimens show elongate *Annularia*-like leaves attached to a nodal diaphragm of a *Calamites* stem e.g., Figure 18d. Such whorls are impossible to assign to any of the species based on leafy shoots and so are here referred to simply as *Annularia* sp.

***Asterophyllites charaeformis* (Sternberg) Göppert in Wimmer, 1844 (= *Bechera charaeformis* Sternberg, 1825)**

The leaves are c. 3 mm long and in whorls of six or less separated by internodes about 3 mm long (Figure 18e). It is a very common species occurring throughout the Langsettian to Bolsovia of the British coalfields (Crookall, 1969; Figure 18e).

***Asterophyllites equisetiformis* Geinitz, 1855**

This species is identified by having whorls of 10 or more than 10 leaves that are much larger than those of *A. charaeformis*. It is a very common species occurring throughout the Westphalian in the British coalfields (Crookall, 1969; here Figure 18f).

3.5.3 | Calamitalean cones

***Palaeostachya ettingshausenii* Kidston, 1903**

Palaeostachya cones are identified by having their sporangiophores attached in the axils of the bracts (Figure 19a). There are two specimens whose general size and bract arrangement make them closely comparable with specimens figured as *P. ettingshausenii* by Kidston (1903) and Crookall (1969). The sporangia have yielded spherical, smooth-walled spores with a small triradiate mark. Crookall (1969) recorded this species as fairly common from the Langsettian of South Staffordshire and Duckmantian of Co. Durham and, more importantly, Shropshire, which is an extension of the Flint coalfield.

***Calamostachys* sp.**

A single, much smaller cone than those referred to *P. ettingshausenii* is too poorly preserved for identification to species. It does have its sporangiophores attached directly to the cone axis showing that it should be referred to the genus *Calamostachys* (Figure 19b).

3.6 | Sphenophylls

3.6.1 | *Sphenophyllum majus* (Bronn) Bronn, 1834 (= *Rotularia major* Bronn in Bischoff, 1828)

The wedge-shaped leaves have a straight or slightly concave margins, and acuminate teeth on the distal margin. The larger specimens have a median cleft for one-third of the leaf length. Crookall (1969) described it as occurring in most British coalfields, very rarely in the Langsettian and Duckmantian, fairly common in the Bolsovia and extremely common in the Asturian (Figure 20a,b).

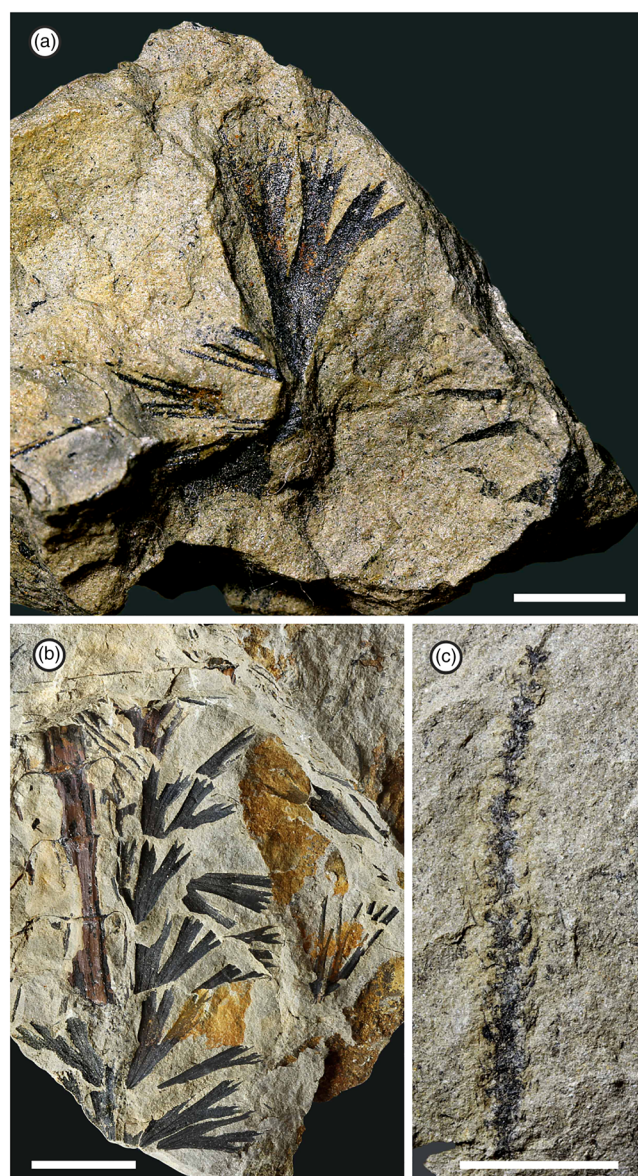


FIGURE 20 Sphenophylls. (a,b) *Sphenophyllum majus* (Bronn) Bronn; (a) 2013.43G.192, bed C4, scale bar = 5 mm; (b) 2013.43G.198, bed C6, scale bar = 10 mm. (c) *Sphenophyllostachys* sp., 2013.43G.249, bed C4, scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

3.6.2 | *Sphenophyllostachys* sp.

There are a number of very small cones e.g., Figure 20c that we tentatively assign to *Sphenophyllostachys* Seward, 1896, but attempts to prepare spores have failed.

3.7 | Ferns

3.7.1 | *Zeilleria* Kidston, 1884

Zeilleria fosteri n. sp.

Diagnosis Vegetative fronds at least bipinnate, 107 mm long and 33 mm wide, pinnule up to 27 mm long. Rachis 0.5 mm wide, smooth. Pinnae alternate, attached at c. 5–15° to midrib, with dissected pinnules attached to midrib at angles between 20° and 85°. On larger pinnae, the pinnules themselves can be alternately divided, up to several times. Individual pinnules narrow basally with wider rounded or blunt apices. Pinnules with a single basal vein alternately branching, with subsidiary branching in the largest pinnules. Veins continue to the tips of the pinnule lobes.

Immature synangia pedunculate with thin stalks up to 2.5 mm long, oval to slightly rectangular in outline, c. 2.2 mm long, 2 mm in diameter, slight indentations showing the positions of at least 6–8 sporangia. Mature fertile frond tripinnate at least 55 mm long and 38 mm wide. Main rachis smooth, 2 mm broad. Pinnae rachises smooth, attached between 32° and 50°. Pinnules replaced by single synangium on short stalks, 3.4–4.0 mm wide and 3.0–3.2 mm high. Mature synangia opened showing individual sporangia, 0.9–2.1 mm long and 0.3–0.5 mm wide, fused together at their base. Each sporangium contains roughly spherical, thin walled spores 49–62 µm in diameter with a well-developed trilete mark about 2/3 of the spore radius. The spore surface is microgranulate, becoming finer on the proximal faces.

Holotype NMW 2013.43G.349 (Figure 21a).

Etymology Named after Andrew Foster, the Director of Parkhill Estates/Brymbo Developments Ltd who has supported both research on the Fossil Forest and its conservation for the future.

Comparisons Carboniferous fern fronds with small, digitate pinnules and synangia borne terminally on the lobes are assigned to the fossil-genus *Zeilleria*. However, the Brymbo specimens differ from any of the previously published species, and so we are proposing here a new species, *Z. fosteri*. *Zeilleria frenzlii* (Stur) Kidston, 1884, is most similar but has larger pinnules with more slender lobes than *Z. fosteri*. The Brymbo specimens also yielded trilete, albeit much smaller spores. The type species *Zeilleria delicatula* (Sternberg) Kidston, 1884, has similar sized pinnules, but unlike *Z. fosteri*, they are borne on rachises that are narrowly winged; the spores of *Z. delicatula* are unknown. *Zeilleria hymenophylloides* (Kidston) Kidston, 1884, also has narrowly winged rachises and much smaller sporangia that contain monolet spores. *Zeilleria avoldensis* (Stur) Kidston is quite different from the Brymbo species in having pecopteroid pinnules and sporangia with monolet spores (Thomas & Crampton, 1971); Dalinval (1960) has placed

Z. avoldensis in a separate fossil-genus, *Bertrandia* (Figures 21a–c, 22a–d, 23a–e, 24a–d, and 25a–c).

3.8 | Pteridosperms

3.8.1 | *Karinopteris* Boersma, 1972

Karinopteris jacquotii (Zeiller) Boersma, 1972 (= *Diplotmema jacquotii* Zeiller, 1888)

There are 19 pinna fragments with the distinctive subtriangular, rounded pinnules of this species (Figure 26a,b). It is a generally rare species but has also been reported from the Duckmantian and Bolsovian substages of Nord-Pas-de-Calais (Danzé-Corsin, 1953; Zeiller, 1888), the Netherlands (Boersma, 1972), the Ruhr (Huth, 1912), and northern England (Kidston, 1925).

3.8.2 | *Alethopteris* (Sternberg, 1825) Zoderow & Cleal, 1998

Alethopteris urophylla (Brongniart) Goeppert, 1836 (= *Pecopteris urophylla* Brongniart, 1834)

The four fragments of alethopterid found at Brymbo have very slender pinnules that somewhat resemble *Alethopteris decurrens* (Artis) Goeppert, but the veins are not as widely forking as normally seen in that species (Figure 26c). They can instead be compared with the more slender pinnule forms of the widely occurring species *A. urophylla*, such as figured by Wagner and Álvarez-Vázquez (2008, figures 8–9). Although widely misidentified in the literature (usually as *Alethopteris lonchitica* Sternberg), Wagner and Álvarez-Vázquez (2008) have shown this species to be very widely distributed in North America and Europe in strata of Kinderscoutian to early Bolsovian age.

3.8.3 | *Neuropteris* (Brongniart) Sternberg, 1825 emend. Cleal, Shute & Zoderow, 1990

Neuropteris semireticulata Josten, 1962

These specimens e.g., (Figure 26f,g) are clearly of the *Neuropteris obliqua* (Brongniart) Zeiller, 1888/*N. semireticulata* complex, and the flexuous, tending to pseudo-anastomosed veins places it in the latter species. Also present is a cyclopteroid pinnule that was probably from the basal part of the *N. semireticulata* frond (see Figure 26f). This species is widespread in the middle Duckmantian to upper Bolsovian substages of Britain, including the South Wales and the Central Pennines basins, the Ruhr Coalfield in Germany, Nord-Pas-de-Calais in France and Lublin in Poland (Cleal & Shute, 1995).

3.8.4 | *Paripteris* Gothan, 1941

Paripteris pseudogigantea (Potonié) Gothan, 1953 (= *Neuropteris pseudogigantea* Potonié, 1893)

As is normal with this species, it is represented here by isolated linguaeform pinnules with a dense venation and a well-developed midvein that extends for most of the pinnule length; the pinnules are typically more or less symmetrical about the midvein (Figure 26h). This widespread species is also

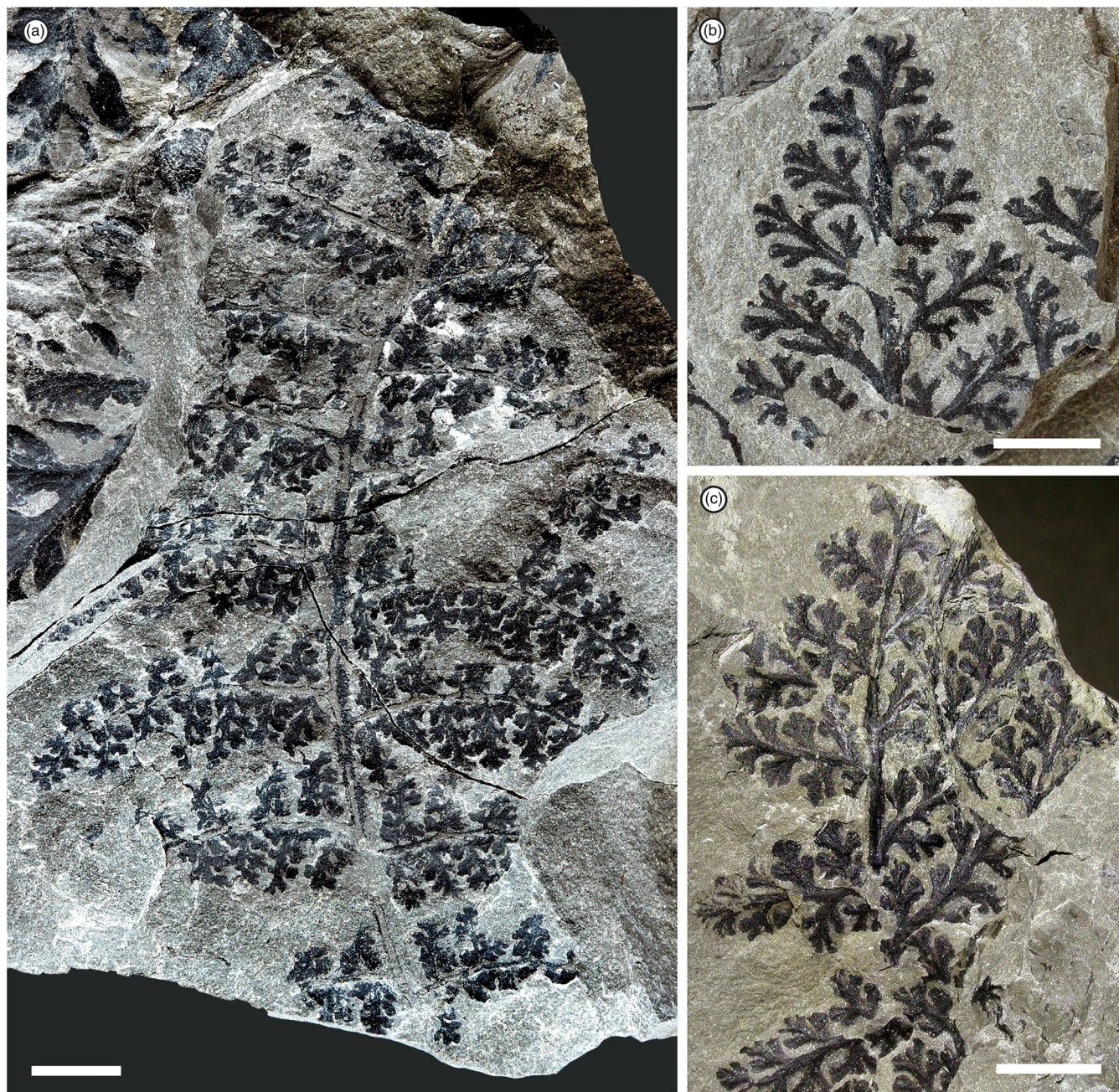


FIGURE 21 *Zeilleria fosteri* n. sp., overview of the morphology of the vegetative fronds; scale bars = 5 mm; bed C4. (a) Holotype, the largest frond fragment, 2013.43G.349. (b) Fragmentary example of smaller pinnules, 2013.43G.345. (c) Fragmentary example of larger pinnules, 2013.43G.340 [Colour figure can be viewed at wileyonlinelibrary.com]

found in the Duckmantian and Bolsovian substages of South Wales and the Central Pennines basins in Britain, northern Spain, Nord-Pas-de-Calais in France, the Ruhr and Saarland basins in Germany, Lublin in Poland and the Donets in Ukraine (Cleal & Shute, 1995).

3.8.5 | Medullosalean fructifications

Aulacotheca elongata (Kidston) Halle, 1933 (= *Rhabdocarpus elongata* Kidston, 1886)

Associated with the alethopterid fragments is a cigar-shaped structure (Figure 26d) that is almost certainly the remains of a pollen-organ that was probably originally attached to the same fronds. It has been

assigned to *A. elongata* because of its shape, although it is a little larger than the specimens figured by Crookall (Crookall, 1976, pl. 173, figures 17–18). Pollen-organs of this type have not been extensively studied and so their distribution is not well understood. The type originated from the Langsettian of Scotland (Crookall, 1976).

Trigonocarpus sp.

Also associated with the *Alethopteris* fragments are large seeds/ovules, one of which shows a marked longitudinal rib. The size, the presence of at least one longitudinal rib and the association with alethopterid foliage clearly points to these being *Trigonocarpus* (Figure 26e).

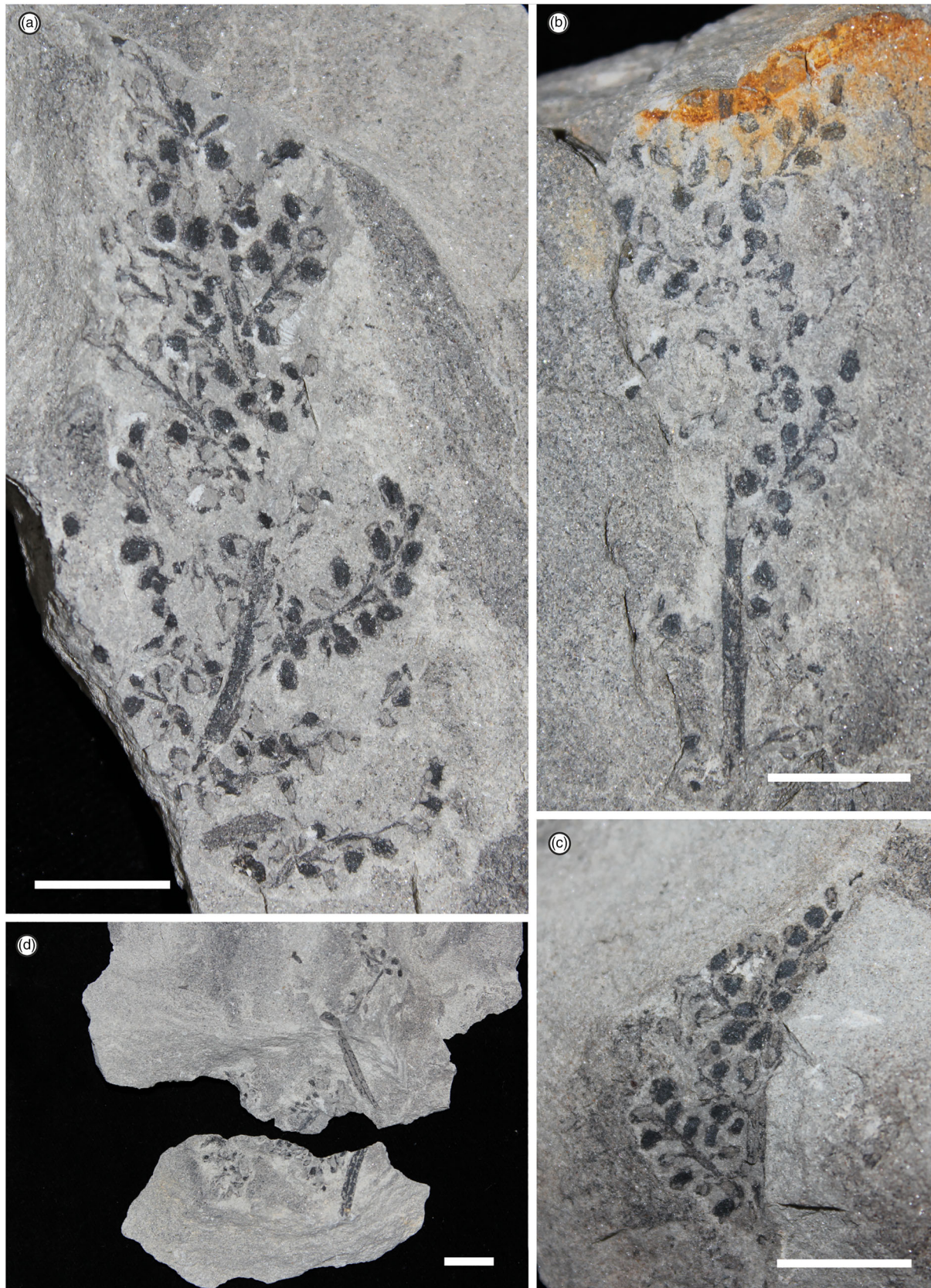


FIGURE 22 *Zeilleria fosteri* n. sp., morphology of the fertile fronds where pedicellate synangia replace lamina, bed C4, scale bars = 10 mm. (a–c) Synangia clearly attached to smooth rachises; (a) largest fragment, 2013.43G.352; (b) mid-size fragment, 2013.43G.351 (part); (c) smallest fragment, 2013.43G.353. (d) Synangial clusters associated with a portion of unattached “grooved” rachis or leaf fragment, 2013.43G.355a,b (part and counterpart) [Colour figure can be viewed at wileyonlinelibrary.com]

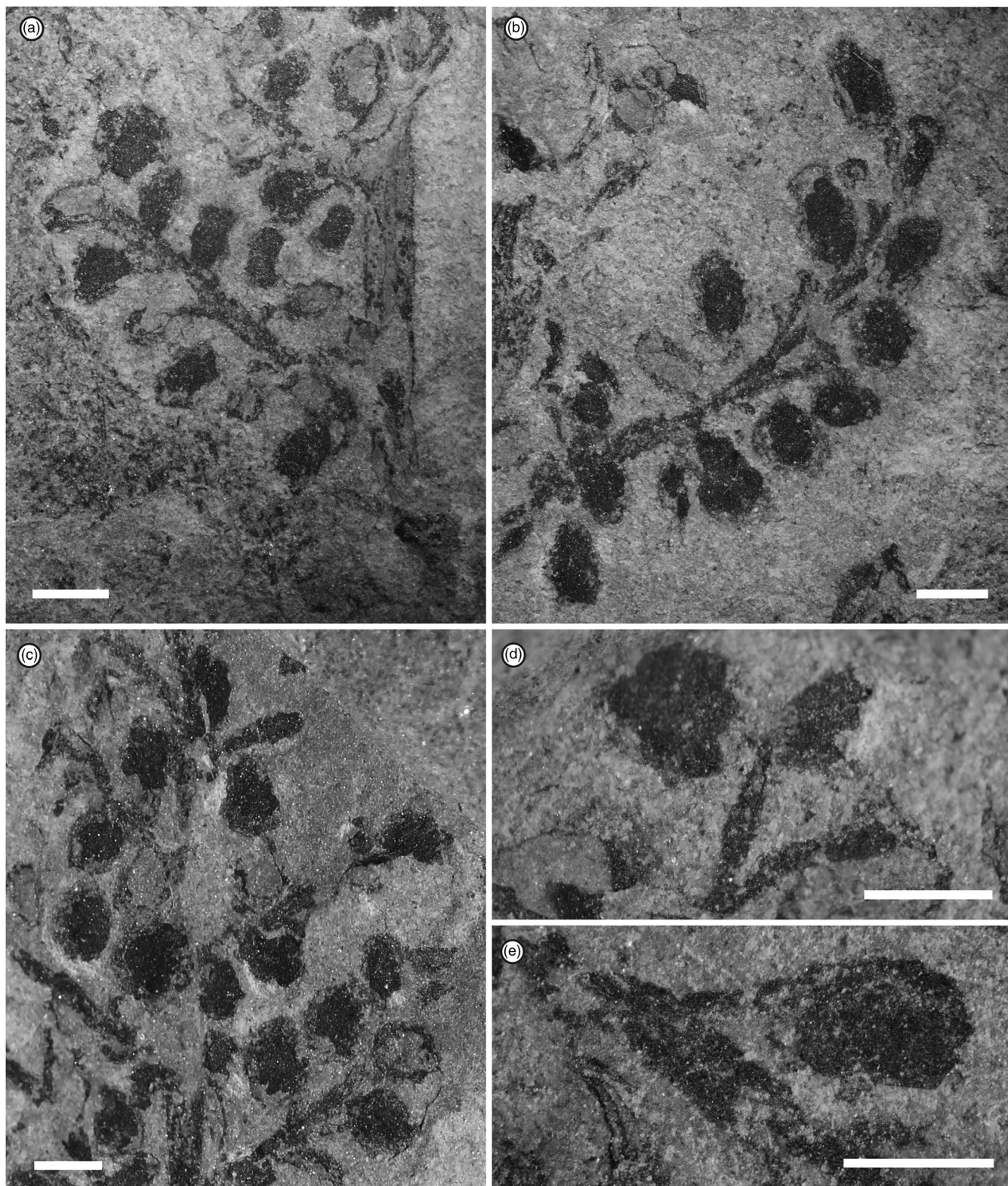


FIGURE 23 *Zeilleria fosteri* n. sp., synangial shape of is dependent on the orientation within the sediment, bed C4, all scale bars = 2 mm. (a,b) laterally compressed synangia appear oval to slightly rectangular in outline, some with a flared base, (a) 2013.43G.353. (b–d) 2013.43G.352. (c) Apically compressed synangia appear circular to oval in outline, 2013.43G.352. (d) Indented synangial outline showing the positions of at least six to eight sporangia, no clear space in the centre of the synagium, 2013.43G.352. (e) Pad of tissue above the pendant sporangia no. 2013.43G.351

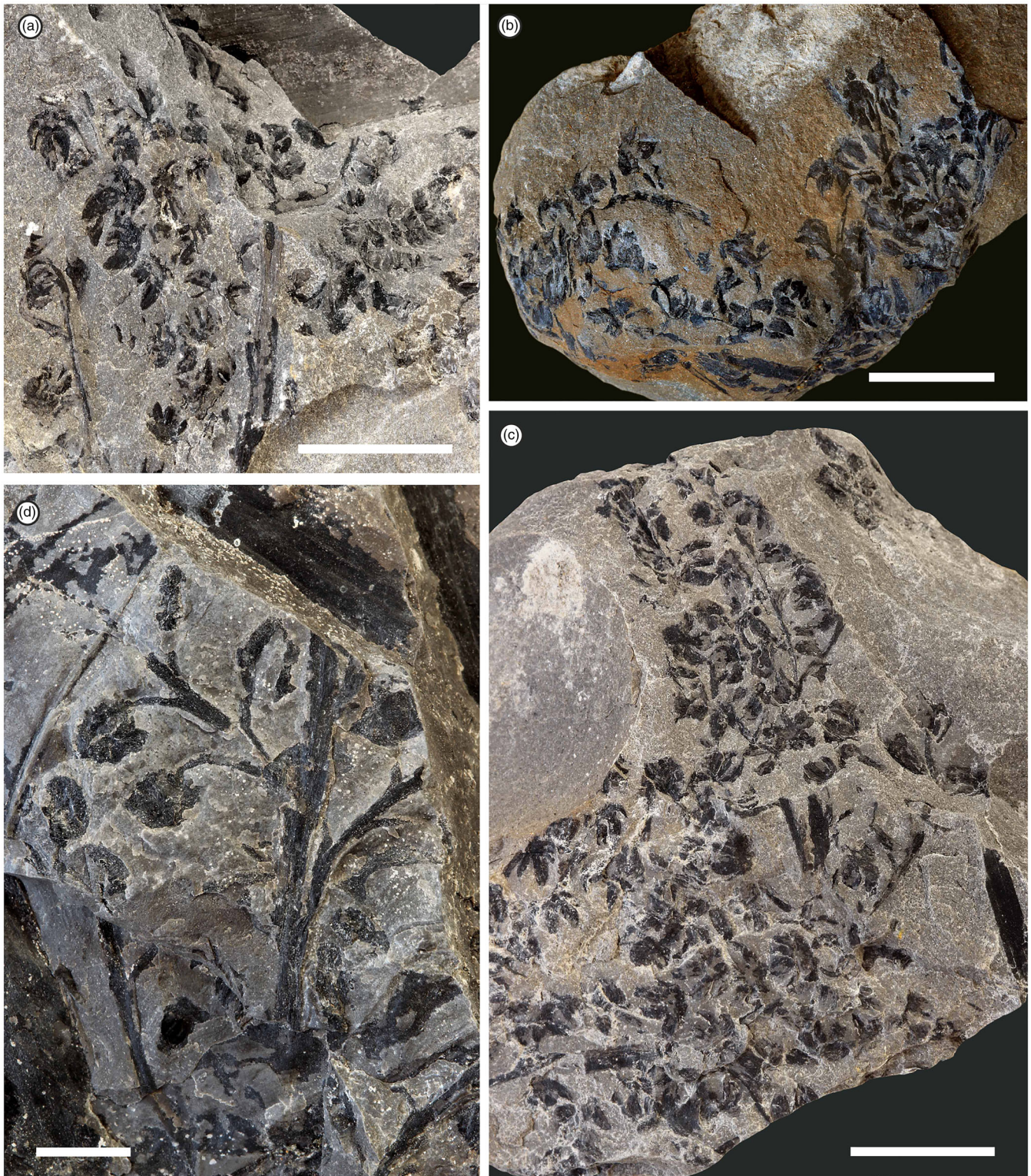


FIGURE 24 *Zeilleria fosteri* n. sp., morphology of the larger, more mature and generally open pedicellate synangial structures, bed C4. (a–c) Laterally compressed synangia, where the synangia are opening and elongate individual sporangia can be seen; (a) 2013.43G.335, scale bar = 5 mm; (b) 2013.43G.338, scale bar = 10 mm; (c) 2013.43G.334, scale bar = 10 mm. (d) Oval outlined synangia showing transverse orientation and indentations marking the position of individual sporangia, 2013.43G.332, scale bar = 5 mm [Colour figure can be viewed at wileyonlinelibrary.com]

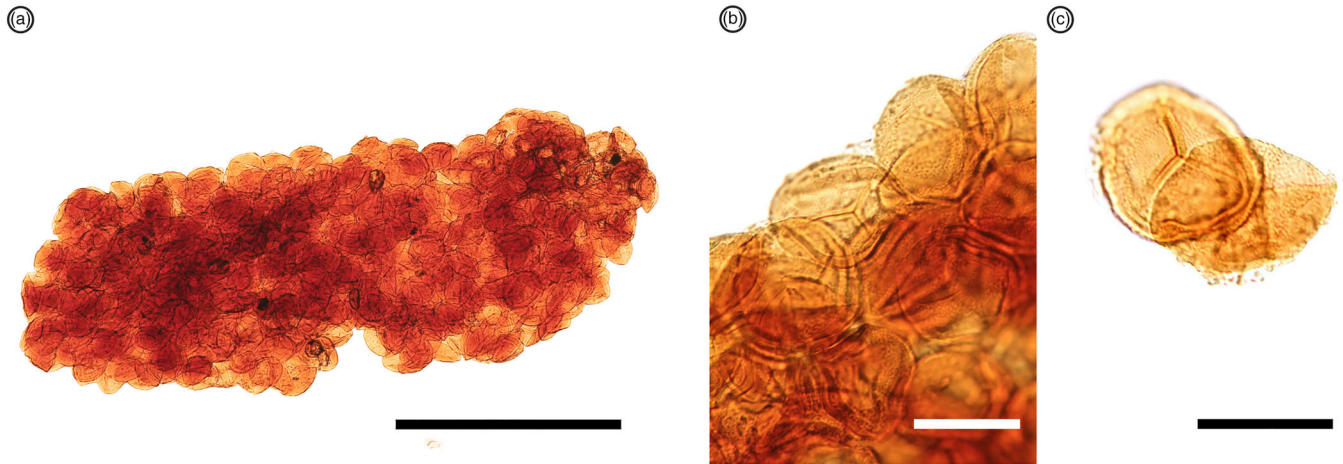


FIGURE 25 *Zeilleria fosteri* n. sp., synangia and in situ spores, bed C4. (a) Isolated sporangium, composite image scale bar = 500 µm. (b) Detail of trilete spores in sporangium, scale bar = 50 µm. (c) Trilete spores showing microgranulate surfaces, with finer granulation on the contact faces, scale bar = 50 µm [Colour figure can be viewed at wileyonlinelibrary.com]

3.9 | Cordaite foliage and stems

3.9.1 | *Cordaites* sp.

Five fragments of leaf belonging to the fossil-genus *Cordaites* Unger, 1850 and an associated stem were found. Šimůnek (2007) has shown the value of cuticle studies in the distinction of species of foliage, so without any epidermal details it is impossible to identify the *Brymbo* specimens at this time (Figure 27a,b).

4 | DISCUSSION

4.1 | Palaeoecology

The distribution of the plant fossils as shown in Table 1, combined with the information about the sedimentology (Figure 2), gives an unparalleled opportunity to see the patterns of vegetation dynamics in the Pennines Basin during middle-late Duckmantian times. A coupling of changing climate and eustatic sea-levels is now widely believed to have had at least some influence on plant distribution in the lower delta-plain ("cyclothem") sequences of North America (e.g., Falcon-Lang & DiMichele, 2010). However, in higher delta-plain settings such as the Pennine Basin, autocyclic sedimentation dynamics and extraneous events such as storms were more significant factors (Gastaldo, 1985a; Thomas & Cleal, 2015).

For long periods of time, the area was covered by extensive forests that generated peat at near water level (Gastaldo, 1985b; White, Gibling, & Kalkreuth, 1994). These peats have subsequently changed into seams of coal. Trying to estimate the time represented by a coal seam is difficult. Rates of peat accumulation in modern-day tropical and subtropical settings varies substantially depending on the setting, from between 0.2 and 6 m every 100 years (Dommain, Couwenberg, Glaser, Joosten, & Suryadiputra, 2014; Frazier & Osanik, 1969; Frazier,

Osanik, & Elsik, 1978). However, different types of plant were growing in these modern-day swamps to those of the coal swamps. The different growth rates between these types of plants make such comparisons rather tenuous. An additional complication is the subsequent compaction, where 7 m of peat may have been reduced to as little as 1 m of coal (Shearer & Moore, 1996; Taylor et al., 1998; Teichmiller, 1989). There were also substantial time gaps represented by the frequent hiatus-surfaces within the coal seams (Jerrett, Davies, Hodgson, Flint, & Chiverrell, 2011; Jerrett, Flint, Davies, & Hodgson, 2010) and possibly between the coal and the underlying seat earth (Scott & Stephens, 2015). Nevertheless, the rate of coal accumulation has been estimated at between 3 and 14 cm per 1,000 years (Broadhurst & France, 1986; Large & Marshall, 2014; White et al., 1994), and so, based on this, in the current paper, we take 1 m of coal to represent a mean value of about 10,000 years.

Coal seams are separated by fluvio-deltaic deposits. The eustatic flooding events that resulted in the cyclothems seen in lower delta-plain settings (e.g., in the Illinois Basin of North America and the Donets Basin in Ukraine) occasionally also impinged on the upper parts of the delta plain, resulting in marine bands that have been extensively used for stratigraphical correlation (e.g., Calver, 1968; Waters & Condon, 2012). In modern-day settings tidal effects can extend for hundreds of kilometres (Schubel, 1984) and that wave processes and turbidity in the centre of channels keeps mud in suspension that eventually results in mud deposits accumulating at 0.1 m in a week (Harris et al., 2004). In upper delta-plain settings such as the Pennines Basin (Fielding, 1984b), however, deposition was more strongly influenced by autocyclic processes such as fluvial channel overbank and crevasse-splay flooding, and channel avulsion (Fielding, 1984a, 1984b, 1986). Thomas and Cleal (2015) have suggested that tropical storms or cyclones may also have overtopped or destroyed the levees, flooding the swamps as well as wrecking much of the vegetation. These sedimentary processes resulted in much more rapid deposition rates than the rate of coal accumulation (Cleal & Thomas,

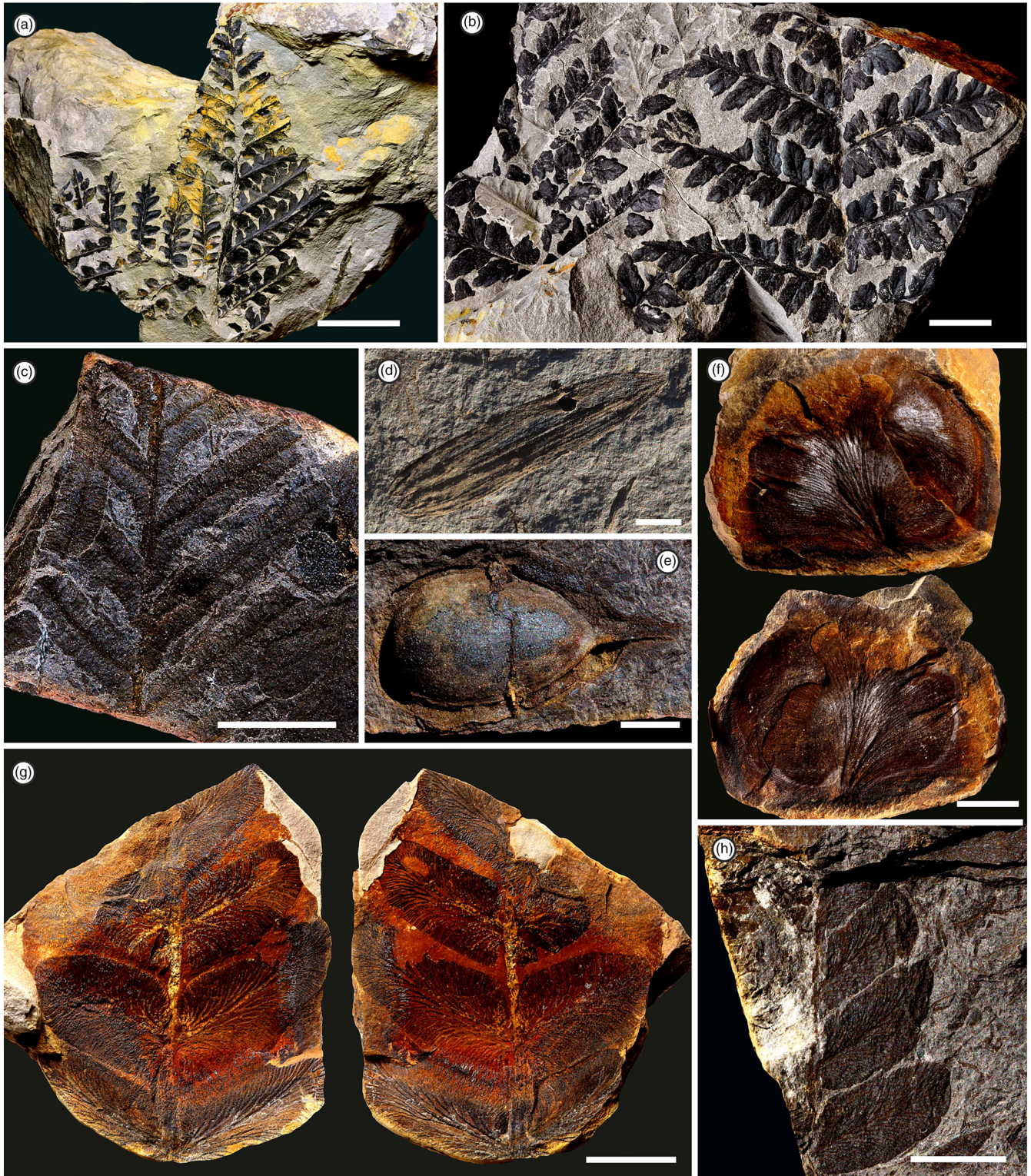


FIGURE 26 Pteridosperms, all scale bars = 10 mm, except (a) = 20 mm; all from bed C4, except (d) and (g), which are from bed Y4. (a,b) *Karinopteris jacquotii* (Zeiller) Boersma; (a) 2013.43G.208; (b) 2013.43G.219. (c) *Alethopteris urophylla* (Brongniart) Goeppert, 2013.43G.178. (d) *Aulacotheca elongata* (Kidston) Halle, 2013.43G.239. (e) *Trigonocarpus* sp. 2013.43G.303 (f,g) *Neuropteris semireticulata* Josten; (f) enlarged pinnules from proximal part of frond, 2013.43G.185; (g) apical portion of frond, 2013.43G.188. (h) *Paripteris pseudogigantea* (Potonié) Gothan, 2013.43G.172 [Colour figure can be viewed at wileyonlinelibrary.com]

2001), and it is now thought that most of the time represented in sequences such as seen in the Pennines Basin is taken up by the coals (Cleal & Thomas, 2001; Scott & Stephens, 2015).

The Brassy Coal (B1) at Brymbo (not presently visible) represented a period of stability that was followed by an influx of dark shale (B2) which yielded seven fragments of lycophytes including the relatively

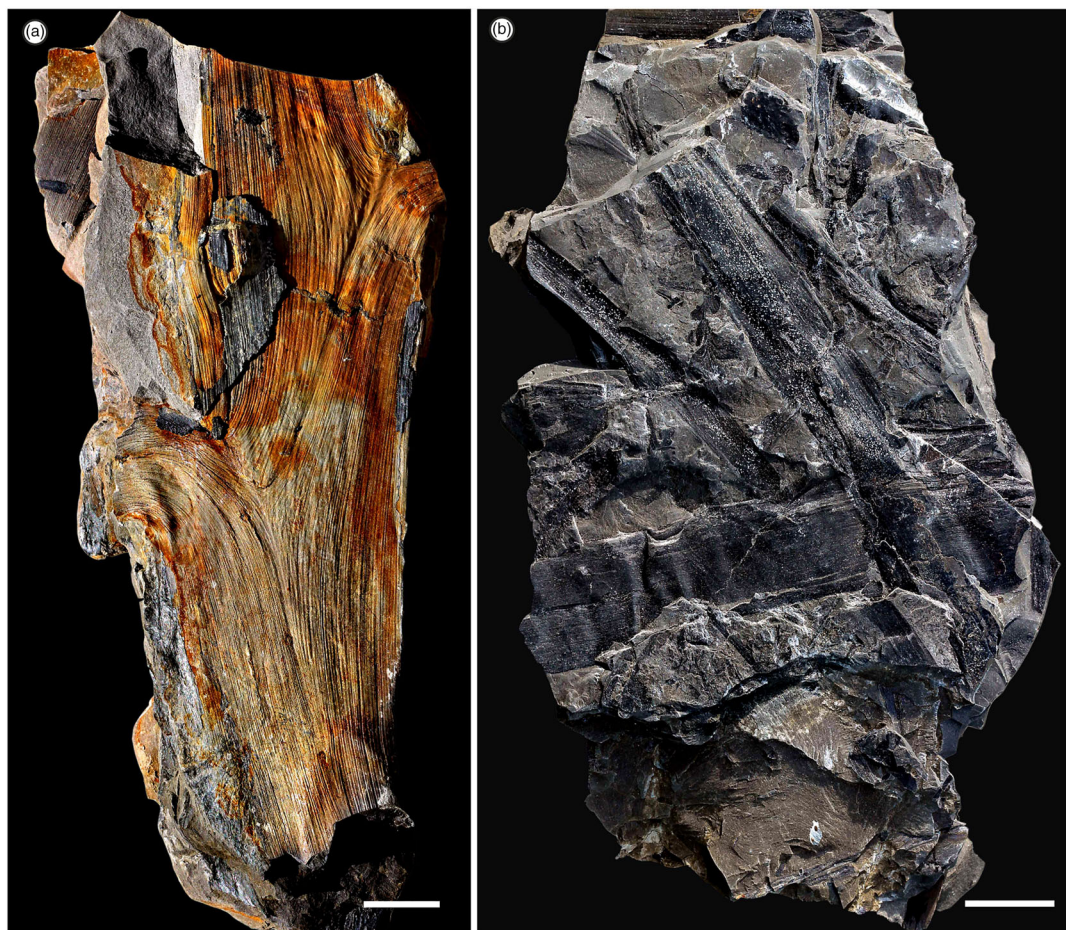


FIGURE 27 *Cordaites* stems and leaves, bed C4, scale bars = 20 mm. (a) stem remains, 2013.43G.155. (b) *Cordaites* Unger leaves, 2013.43G.156, bed C4 [Colour figure can be viewed at wileyonlinelibrary.com]

rare *O. feistmantelii*. This was followed by a break in sedimentation, and then an influx of light grey muds containing portions of *Stigmara* that represents the palaeosol (B3) on which the Crank Coal (C1) developed, the latter representing about 8,000 years.

The stable swamp forest community was abruptly halted by the influx of large amounts of iron-rich fine sediments that after compaction resulted in over a metre of dark shale (C2) in which siderite concretions containing abundant plant remains developed. Similar siderite concretion bearing deposits are known in other coal-bearing sequences such as Mazon Creek in Illinois, USA (Darrah, 1969; Nitecki, 1979; Wittry, 2006), Nova Scotia in Canada (Zodrow & Cleal, 1998), and central England (Kidston, 1914) and are likely to be the result of subsidence of the swamps to a depth where conditions were anoxic with low Eh and high pH (Kholodov & Butuzova, 2008; Krumbein & Garrels, 1952). The formation of such nodules appears to have been stimulated by the formation of siderite on the surface of organic matter below the surface of the sediments (Baird, 1977; Woodland & Stenstrom in Nitecki, 1979). Curtis, Coleman, and Love (1986) suggested that siderite is formed through the combined effects of iron reduction and bacterial methanogenesis of organic compounds. Such a process at Brymbo entombed many fragments of the plants that were killed by the sudden inrush of sediments before they could

decay. However, not all concretions at Brymbo contain plant or animal remains possibly having been formed around minute fragments of organic matter. Clements, Purnell, and Gabbott (2018) noted barren concretions at Mazon Creek and suggested that prolonged aerobic bacterial respiration, before entombment in siderite, would have allowed organic material to decay.

The flood disrupted the ecosystem resulting in a mixture of aerial parts of the plants growing within the swamps and those living on the adjacent drier levees. Following this period of disruption, a brief period of stability allowed the swamp vegetation to recover enough to form peat that on compaction gave a narrow, 15 mm dark coal parting (C3). But another influx of a large amount of sediment resulted in 2 m of siltstone grading upwards into silty sandstone (C4) suggesting that sedimentation occurred over a period of time; otherwise, the coarser silty sandstone would have settled first. The fact that calamite stems were preserved as casts in their positions of growth shows that the sand came in, covered the area, and accumulated very rapidly. Also present in this interval is the most diverse plant fossil assemblage found at Brymbo, remarkable in particular for including *Ulodendron*, *Omphalophloios*, two species of *Lepidophloios*, the distinctive *Lepidondendron ophiurus*, together with *Sphenophyllum*, two species of pteridosperms, and one specimen of *Cordaites* leaf.

The following layer (C5) is a thin (25 mm) grey mudstone crowded with lycophyte shoots cones and dispersed megaspores, calamite branch casts and some very small calamite cones. There then follows an arenaceous sequence that fined upwards that probably represented a flood-event. At the base is a 0.8 m layer of near white sandstone (C6) with ironstone staining in the joints. There are clusters of *Calamites* stems in their original growth position, with some of them tilted, showing the direction of flow of the sediments to be from the north-west. At the eastern edge of the site these are flattened casts of lycophyte stems, *Calamites* and drifted tangles of other plants. This is then followed by a 2-m-thick light yellow thinly bedded sandstone also containing many *Calamites* in growth position (C7). There are a number of casts of *Stigmara* towards the top of the unit with one being 8 m long with no indication of tapering at either end.

A 30 mm seat earth (C8) lies underneath the 1 m lower section of the two-yard coal (Y1) which is split from the upper 1.5 m section (Y3) by another 0.30 m seat earth of light grey soft mudstone (Y2). Together, this coal probably represents 25,000 years of forest cover. This coal interval is overlain by 0.15 m of fragmented ironstone (Y4) with lycophyte bark on the lower surface, suggesting these fragments were lying on the surface of the peat when it was flooded with iron-rich sediments.

4.2 | Biostratigraphy

The presence of *N. semireticulata* and *Paripteris pseudogoigantea* strongly indicates the *Paripteris linguaeifolia* Zone of Wagner (1984), which in turn indicates a late Duckmantian or Bolsovian age. Cleal and Thomas (1994) divided this zone into subzones based on a major change in the floras in the lower to middle Bolsovian Substage. None of the usually abundantly found species that appear at this level (e.g., *Laveineopteris rarinervis* [Bunbury] Cleal et al., *Annularia sphenophylloides* [Zenker] Gutbier, and *Sphenophyllum emarginatum* [Brongniart] Brongniart) occur at Brymbo, which tends to suggest that the flora here belongs to the lower (*N. semireticulata*) of these subzones. This would be compatible with a late Duckmantian age for the Brymbo strata. There is no evidence of the species whose presence would indicate the Asturian *Linopteris obliqua* Zone, notably *Neuropteris ovata* Hoffmann.

4.3 | Comparisons

The only other well-documented *N. semireticulata* Subzone flora from Central Pennine Basin is from Howgill Head Quarry in Whitehaven, from the West Cumberland Coalfield (Thomas & Cleal, 1993). There are a number of pteridosperm species in common between the two floras, such as *A. urophylla*, *P. pseudogigantea*, and *N. semireticulata*, but the sphenophytes and ferns are quite different; it is notable, for instance, that some of the key species used to indicate the *N. semireticulata* Subzone (e.g., *Annularia sphenophylloides*) are absent from the Whitehaven flora but present at Brymbo. Also, there is a significant difference in the overall balance of the floras, with Brymbo

having a much greater diversity of lycophytes and a lower diversity of ferns and pteridosperms compared with the Whitehaven flora. This may be partly related to the different lithologies in which the floras occur: The Whitehaven flora occurs in a relatively light grey, somewhat silty matrix probably of a crevasse-splay or overbank deposit; the most fossiliferous layer at Brymbo is in darker grey mudstones with ironstone nodules probably of lacustrine origin.

There are a few other records of *N. semireticulata* Subzone floras from northern England, notably from Yorkshire and Northumberland (reviewed by Cleal, 2018), but none have been described in detail. The Brooch Coal of the South Staffordshire Coalfield has yielded a flora probably from the lower *N. semireticulata* Subzone (Cleal, 2008a), but again, there is no detailed taxonomic analysis. There are no well-documented records of floras of this age from southern England.

In South Wales, *N. semireticulata* Subzone floras are known from several levels, perhaps most notably the roof shales of the 4 ft and Gorllwyn seams of the South Wales Middle Coal Measures (Cleal, 2007). None of these South Wales floras has been the subject of an individual taxonomic study, so a detailed comparison is difficult, but it is notable from the analysis in Cleal (2007), that there is a peak in diversity at the 4 ft Seam, mainly caused by a temporary rise in the number of non-marattiale fern species; no comparable peak in fern diversity is evident at Brymbo.

Elsewhere in Europe, similar-aged floras from lowland paralic settings are known from the Faisceau de Pouilleuse of the Nord-Pas-de-Calais Coalfield (e.g., Laveine, 1986) and the Horster Schichten of the Ruhr Coalfield (Josten, 1991), but there are no descriptions of representative floras from these intervals to allow proper comparison with the Brymbo flora. It is of note that, according to the records summarized by Laveine (1986), many of the key species found at Brymbo only occur in the topmost part of the subzone in Nord-Pas-de-Calais (e.g., *Annularia sphenophylloides* and *N. semireticulata*). In the Ruhr, however, the species are more widely distributed in the Horster Schichten. Similar-aged floras also occur in the upland-wetland basins (*sensu* Thomas & Cleal, 2017) of Euramerica, such as Saar-Lorraine (e.g., Laveine, 1989) and Western and Central Bohemia (e.g., Šimůnek in Pešek, 1994), but these tend to have very distinctive floras from those of the lowland paralic basins such as seen at Brymbo (e.g., Cleal, 2008b, 2008c).

5 | CONCLUSIONS

This is one of the best late Duckmantian fossil macrofloras known from Britain and arguably the most characteristic of the *N. semireticulata* Subzone. There are other floras known of similar age, such as from the West Cumberland, South Wales, Nord-Pas-de-Calais, and the Ruhr, but few have been subject to detailed taxonomic analysis. Moreover, none are from conserved sites, leaving the Brymbo flora as the only one where the geological context of the floras can be seen and where there is thus potential for further collecting.

Careful recording of the plant fossils has enabled different assemblages to be recognized from the various strata enabling us to make tentative ecological interpretations. The ability to see the changing sediments between two coal seams together with their differing assemblages of plant fossils, lycophyte stems, and *Calamites* in their original growth positions makes it a unique and valuable site. It is without doubt of both national and international importance being an SSSI and a new GCR site. This is an example of how the GCR is being kept up to date as new information become available. For further information on the British GCR and international palaeobotanical sites, see Cleal and Thomas (1998) and Thomas and Cleal (2005, 2012).

The site will potentially produce more information in the future and the long term preservation and development of the site will increase its value for research, teaching, and geological tourism (Thomas, 2016).

CONFLICT OF INTEREST

The authors state that they have no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Thomas BA, Appleton P, Cleal CJ, Seyfullah LJ. The distribution of plant fossils and their palaeoecology in Duckmantian (Bashkirian, Lower Pennsylvanian) strata at Brymbo, North Wales, UK. *Geological Journal*. 2019;1–29. <https://doi.org/10.1002/gj.3529>